tion was made by brushing the uninjured leaves with the liquid, by scratching the leaves with a needle wetted in the liquid, and by injecting the liquid hypodermically into the leaves, new stem growth, and older stems. Control plants were similarly treated but using sterile water in place of the liquid obtained from the crushed leaves. The experimental plants were all periodically examined throughout the whole of the growing season. In all this time there were no observable indications of the symptoms of graft-blight. This failure to transmit the blight is further evidence of its abiotic nature.

With the same purpose in mind still another experiment was undertaken, one which would make sure that the disease could not be referred to a virus disease in the privet understock. It is known that there is a virus disease of the California Privet in the southern United States. So a number of privet plants were obtained from a Georgia nursery in the heart of the region of this disease. Healthy scions of Lilac grafted upon these stocks developed the symptoms of graft-blight which are usually associated with the use of California Privet of whatever source as an understock. As a second part to the experiment with this same lot of Privet, some of their buds were inserted into healthy lilac shoots. They grew satisfactorily but neither was there any transmission of visible blight to the lilac stocks, nor did the grafted buds at any stage of their subsequent development show any signs of disease. Were there present in these Privets a virus disease communicable by grafting, it is to be expected that it would likewise be transmitted by budding in this fashion.

There still remains to be described a set of experiments of the same general import but dealing with the phenomenon of variegation as it occurs in certain varieties of Lilacs. It is known that a number of chloroses and variegations in plants are contagious, and presumably due to the activity of some ultramicroscopic principle. This situation has been found to obtain in some of the Oleaceae, as in *Fraxinus* and *Ligustrum* (3, 4), and so might very well be true of some of the Syringas. Three variegated varieties of Lilac, namely, *Syringa vulgaris* var. *aurea*, *S. vulgaris* var. *aucubaefolia*, and *S. emodi* var. *aurea*, were examined. While all of them showed a yellowing of the foliage, in no case was it at all comparable to the yellowing of graft-blight. Five scions each of these three varieties were grafted upon healthy lilac plants of varieties susceptible to graft-blight. Thirteen of the fifteen grafts were successful; in the other two (*S. emodi aurea*) the scions failed to unite with the stocks. In no case was there evident throughout the season after grafting any symptom of yellowing in the shoots from the stocks. All the plants remained perfectly healthy. The evidence from this experiment shows that the chlorosis in these variegated varieties is not communicable to *Syringa vulgaris* by grafting, and that it is entirely distinct from graft-blight.

From the abundant evidence presented it is concluded that graft-blight is not caused by any pathogenic or contagious principle.

B. RELATION OF GRAFT-BLIGHT TO EXTERNAL ENVIRONMENT

Since graft-blight has been shown to be abiotic in nature, it is next necessary to consider whether the disease might not be due to some unfavorable influence in the external environment. It is apparent that factors of the external environment which might conceivably bring about a diseased condition in Lilacs of the type of graft-blight are the climate, the physical and chemical constitution of the soil, and the conditions of soil and atmospheric moisture. With regard to the first, it will at once be seen that since the distribution of graft-blight coincides with the range of climatic conditions most suitable for lilac culture, it is inconceivable that graft-blight could be attributed to unfavorable climate.

That the disease might be due to unfavorable soil conditions or constitution was next investigated. It must be borne in mind at the outset that the Lilac in general is extremely tolerant of adverse soil conditions, its popularity to a considerable extent depending upon this adaptive capacity. The last vestige of cultivation in many deserted New England homesteads is the hundred-year-old lilac thicket, which has persisted, even thrived, in spite of the impoverished condition of the soil.

The lilac blight was observed in a wide variety of soil conditions and on soils which showed that the disease could bear no relation to soil fertility or soil acidity. It can be seen in its greatest severity in nurseries where every other species of shrub appears perfectly healthy. Healthy and blighted plants of Lilac frequently grow in essentially the same soil, side by side. The blight was found in nursery plots of a high degree of fertility no less severe than in the field. It was experimentally reproduced in plants growing in well fertilized loam in a greenhouse beside healthy control plants in the same soil. That the disease is independent of the degree of soil acidity was established by pH determinations of soils in which healthy and blighted plants were growing. Severe blight was found in soils ranging in pH from 5.3 to 8.1 with no difference in degree or nature of symptoms in any of these soils. It is entirely improbable that a disease which could occur over a range of pH of this breadth could have been caused by degree of soil acidity or alkalinity.

Since an iron deficiency of the soil is known to bring about a cholorosis of the leaves, a number of plants in the field were treated with varying amounts of iron sulphate. Commercial copperas was used in dosages of 100 to 500 grams per three foot plant, well mixed in the soil. In no case was there any amelioration of the symptoms seen in the subsequent examinations which extended over a period of eighteen months. Control plants similarly treated remained perfectly healthy. Hence it may be concluded from all the foregoing observations that the nature of the soil is not the causative agent of lilac graft-blight. The disease bears no consistent relation to the physical or chemical properties of the soil.

If one considers the possible relation of graft-blight to the water supply, the evidence is more suggestive. The disease was observed during three summers. The summer of 1928 was rather wet in New England. The disease that year was present in destructive measure. The following summer was one of the driest experienced in the same vicinity. The disease was if anything more severe than during the preceding year. During the summer of 1930 there was a subnormal rainfall, but sufficient for most vegetation. There was some alleviation of the symptoms during that summer. But that rainfall is not the determining factor is evidenced by the fact that in both very wet and very dry years the disease still occurs to destructive extent. It should be noted that the water requirements of the Lilac are not extreme. It requires a reasonable amount of moisture, though the soil must be well drained. The blight was found on well drained hillsides under conditions in which the water supply for Lilacs is near an optimum. It was found to an equal extent in moist, shady, lowland nurseries and in the dry soil of hilltops. In experimentally reproduced graft-blight, the plants were in a greenhouse with a somewhat humid atmosphere, and were well watered. Nevertheless the disease was of significant severity under all these conditions. From the foregoing, while it may be concluded that the disease is increased in severity by abnormal dryness and diminished in severity by moderate moisture, yet one cannot attribute to moisture more than a minor contributory significance in the causation of the disease.

As a final check on the influence of external environment on lilac graft-blight, a number of healthy and blighted plants were transplanted into locations somewhat different in soil fertility, water relations, and exposure. Blighted Lilacs were transplanted to the sites of successful plants, and healthy plants were moved to sites where severe blight was prevalent. Typically blighted plants with histories of at least two years of acute symptoms were transferred from their former location, on a well-drained, fertile hillside to: (a) a low, moist, well fertilized nursery bed; (b) an exposed hilltop where the water supply was limited but where there was a healthy old hedge of Lilac over a hundred years of age; (c) a lowland, well-drained nursery bed with light, loamy soil; (d) a greenhouse where they were potted in rich soil and well watered; (e) an upland nursery bed adjacent to healthy, thrifty Lilacs. In addition (f) two blighted plants from a nursery bed with well-drained fertile soil were transplanted to a hillside location surrounded on all sides by excellent healthy lilac plants. The crowns of all these plants were cut back severely at the time of transplanting and the plants well watered for the remainder of the summer. These plants were observed periodically for eighteen months. At the time of writing none has shown its symptoms to be ameliorated to any appreciable extent. Meanwhile six healthy lilac suckers with histories of excellent development were placed in the identical spots vacated by six of the severely blighted plants. These were given the same care as the other transplanted Lilacs. During the eighteen months following the transplantation, these six plants have doubled their former size, and at the time of writing are in excellent health.

These transplantation experiments show even more vividly the independence of the disease on the immediate external environment, and offer a final demonstration that the disease is related directly to the properties of the plants themselves, and only to an inconsequential degree to any external environmental factor.

C. CONSTITUTIONAL WEAKNESS OF CERTAIN LILAC VARIETIES NOT THE BASIS OF THE DISEASE

As a third projected explanation of graft-blight it was suggested that the disease is simply a manifestation of the constitutional weakness of certain newer varieties of *Syringa vulgaris*. During the past two or three decades an increasing number of new horticultural varieties of Lilacs have been originated; these newer varieties have collectively received the somewhat inaccurate name "French Hybrids." The French hybrids are the outcome of selection, the basis of which has been to enhance the beauty and the quantity of bloom. Little attention has been paid in this process of selection to hardihood and vigor in the selected varieties. Hence it is conceivable that these new varieties might be inherently weak in constitution, and that their inability to prosper under conditions usually suitable for Lilacs might result in the symptoms of the disease under consideration. However, the question can be answered by a study of the varieties in which graft-blight is known to occur.

If the disease were found exclusively in the newer French hybrids, then one would have grounds for assuming that their weakness might be responsible for the symptoms. If, on the other hand, the disease could be shown to occur in numerous old, well established, time proven varieties, then one might eliminate the constitutional weakness of the newer varieties as an explanation for graft-blight. A careful study of the distribution of graft-blight among the varieties of *Syringa vulgaris* has brought out clearly that the disease is not restricted to the newer varieties, but that it occurs with destructive frequency in the old, long-established varieties of Lilac which are distinguished by their strength and vigor. A few examples of the occurrence of graft-blight in such vigorous old varieties will serve to illustrate the point.

Lilac graft-blight was observed in 79 of the 238 accepted horticultural and natural varieties of *Syringa vulgaris.* These 79 varieties include the varieties "Perle von Teltow" and "Rubra de Marly" which have been recommended for use in forcing because of their resistance and vigor. The variety "Andenken an Ludwig Spaeth," in which the blight was experimentally reproduced scores of times, is generally conceded to be one of the strongest varieties known. The list of varieties in which graft-blight occurs includes "Azurea plena," "Bicolor," "De Croncels," and "Violacea" (*S. vulgaris* var. *purpurea*), all of which are old horticultural forms which have proved successful for the last eighty years or more. The lists of the best lilac varieties, chosen for strength and vigor as well as for beauty by the lilac connoisseurs Wilson (38), Havemeyer (15), Molyneux (25), and Wister (39) include a number of forms in which graft-blight has been found to occur. Among these varieties are: Archevêque, Belle de Nancy, Capitaine Baltet, Carmen, De Croncels, Henri Martin, Hippolyte Maringer, Jacques Callot, Jules Simon, Mme. Antoine Buchner, Mme. Lemoine, Masséna, Maurice Barrés, Miss Ellen Wilmott, Montaigne, Othello, Rubra de Marly, Victor Lemoine, Ville de Troyes, and Waldeck-Rousseau as well as the variety Necker of *Syringa hyacinthiflora.* In all these varieties graft-blight was seen occurring naturally in Lilacs obtained from commercial nurseries.

The conclusion is obvious. Lilac graft-blight shows no restriction to variety in all the cases that have thus far been investigated, and in particular it may be definitely said that the disease has nothing to do with the alleged constitutional weakness of the newer French hybrid varieties.

To be sure it was observed that some varieties show the effects of graft-blight more than the others. Some nurseries from their experience have already become aware of this fact. By way of example the varieties "Mme. Lemoine" and "Mme. Florent Stepman" show the effects of incompatible grafting to a greater extent than other varieties, as "Diderot." But I am convinced that no variety of *Syringa vulgaris* is immune to the detrimental effects of privet grafting.

D. INCOMPATIBILITY BETWEEN LILAC SCIONS AND PRIVET STOCKS AS THE CAUSE OF LILAC GRAFT-BLIGHT

It was stated in the introduction of this paper that lilac graft-blight is due to an incompatibility between lilac scions and privet stocks when associated in the graft-union. Before considering the proof of the relation of the disease to such an incompatibility, it was first necessary to visualize all the other possible factors which might cause graft-blight and to show in turn that each of these could not stand in causal relation to the disease. This having been done in the preceding subsections, the way is now clear for a detailed statement of the grounds on which the decision is based that graft-blight is caused by such an incompatibility.

The proof of the relation of graft-blight to a lilac-privet incompatibility rests on two main bodies of evidence. In the first place, the correlation between privet grafting of Lilacs and graft-blight was established by an extensive series of experimental lilac grafts in the greenhouse; in the second place, the results obtained from these experimental grafts were confirmed by numerous observations in the field. But before proceeding to a detailed exposition of these experiments and observations, it is fitting to introduce as a preface the circumstances which originally led to a consideration of the relation between graft-blight and the practice of grafting Lilacs upon privet roots.

Lilac graft-blight first came to my attention in the ornamental lilac planting of the Arnold Arboretum. In the year 1928, there were in this collection about 350 lilac plants, 75 of which were showing the typical symptoms of graft-blight. The histories of these 75 Lilacs were studied in detail in conjunction with those of the 275 healthy plants. It was at once apparent that although the diseased plants varied extensively as regarded age, variety, situation, exposure, and soil conditions, they all agreed in one respect, namely, that they had all been propagated by grafting upon Privet. Such was not the case with the healthy plants. The fact that the blighted plants had been grafted upon Privet, as stated in the records, was confirmed in most cases by a direct examination of the root systems.

The sources of these diseased plants were investigated and the results of this investigation are incorporated into Table II.

TABLE II. SOURCES OF 75 LILAC PLANTS, ALL AUTHENTIC CASES OF GRAFT-BLIGHT

Source	Year of Acquisition									
	1929	1928	1927	1926	1925	1924	1923	1922	1921	Total
Nursery "A" . . .	2	32		1	4	1			1	41
Nursery "B" . . .			3	1		19	1			24
Nursery "C" . . .			4		5	1				10
Total	2	32	7	2	9	21	1		1	75

Thus all of the diseased Lilacs came from three nurseries, and it was later ascertained that each of these three nurseries uses the privet method of lilac propagation almost exclusively. It is seen from the table that the majority of these Lilacs came in two shipments, one in 1924, the other in 1928. The shipment from nursery "B" in 1924 originally numbered 74 plants. Nineteen of these are now in the ornamental planting of the Arnold Arboretum and are displaying various degrees of typical graft-blight. Ten more are perfectly healthy. Of the remaining forty-four many were culled out in the years 1924–1928 while a few are still in the nursery beds, too small to be planted out in the ornamental collection. The shipment in 1928 from nursery "A" originally numbered thirty-three plants. At present thirty-two of these are numbered among the authentic cases of graft-blight in this collection. Three of the plants are already dead; others are of miserable appearance. A few will probably ultimately recover.

Working from these observations as a starting point, the problem of graft-incompatibility was put to a test under controlled experimental conditions. A set of experiments was undertaken in 1928 to compare the condition of grafts of the same variety of Lilac grafted upon various understocks as compared with those propagated by cuttings, the plants being all grown side by side under the controlled environmental conditions of a greenhouse. The results were so striking that the experiments were repeated in 1929 on a larger scale, and below will be considered the results of these experimental grafts, which demonstrate beyond question the causal relation of the privet grafting method to lilac graft-blight.

In carrying out these experiments "splice" grafts were used for the most part, although a few of the grafts were of the "whip" type. The appearance of the junction in splice grafts is shown in Figures 4–6. The differences in technique brought about no effect on the success of the union. The grafts were so made that each scion would have two pairs of good buds for development. The unions were bound with raffia and waxed. In no case was the union permitted to be below the soil level. Technically the process of grafting showed a high degree of success; union was accomplished in nearly all cases. The grafted plants were grown in a greenhouse under suitable conditions. Table III presents the results of these experiments. The scions employed were of the variety *Syringa vulgaris*

TABLE III. EXPERIMENTAL OLEACEOUS GRAFTS 1929–1930

Stock:	Number of grafts:	Number of ungrafted controls:	Date of grafting:	Success of graft:
Syringa vulgaris	6 65	6 2	1–25–29 1–21–30	INCOMPATIBILITY NONE. All remaining in excellent health throughout the experiment. Controls healthy. Fig. 4 (Pl. 33) shows a representative specimen.
Syringa japonica	5 14	1 2	1–25–29 1–21–30	INCOMPATIBILITY SLIGHT. Excellent growth but evidence of a mild degree of incompatibility, manifested by a slight flecking of the leaves during the summer. Controls healthy. Illustrated in Fig. 5 (Pl. 33).
Syringa villosa	15	2	1–21–31	INCOMPATIBILITY MODERATE. The growth is weak on this stock, the twigs small, leaves few. Browning of the leaf margins, brittleness of the leaves, and early defoliation mark the graft. Controls healthy.
Ligustrum ovalifolium (This is the stock generally used in commercial lilac propagation where "privet" is indicated. Throughout this paper the term "privet" refers to this species, the California privet.)	6 50	2 3	2–27–29 1–21–30	INCOMPATIBILITY MARKED. During the course of the summer the leaves become wrinkled, thicker, brittle, and spotted with tiny dead areas which mark the early stage of development of incompatibility. The margins of the leaves become dead and torn. However, the growth and general appearance are not usually very bad. All survive the winter. The following year these same symptoms are present and somewhat more marked than the preceding year. These are the typical symptoms as are seen in the field, marking a plant as grafted on Privet and in an early stage of incompatibility. These symptoms have never been seen on an own-rooted Lilac. Controls healthy. This important stage of incompatibility is well indicated in Fig. 4 (Pl. 33), which is a faithful reproduction of one of the plants of this experimental set.
Ligustrum ibota	6	2	1–25–29	INCOMPATIBILITY MARKED. The symptoms here are almost identical with those of the grafts on *L. ovalifolium*. The course of the disease is the same. The remarks applying to one apply to the other equally. Controls healthy.

Stock:	Number of grafts:	Number of ungrafted controls:	Date of grafting:	Success of graft:
Ligustrum ibolium	6	2	1–25–29	INCOMPATIBILITY MARKED. Symptoms identical with those of the two preceding with the exception that here the blight is slightly less apparent. The condition the second year is somewhat better. However, none of these stocks is to be considered as a desirable understock for Lilac. Controls healthy.
Ligustrum vulgare	6	2	1–25–29	INCOMPATIBILITY MARKED. Symptoms similar or identical to those of the other species of Privet above. Controls healthy.
Ligustrum vulgare var. "Lodense" (Horticultural variety)	9	2	1–21–30	INCOMPATIBILITY MARKED. Symptoms similar to those of *L. ovalifolium* but incompatibility more pronounced. This stock is intermediate in its incompatibility between the species immediately preceding and following. Controls healthy.
Ligustrum obtusifolium var. *Regelianum*	11	2	1–21–30	INCOMPATIBILITY MARKED. Symptoms as in all the preceding species of privet but more severe than any other yet considered. Controls healthy.
Ligustrum amurense	6 45	2 9	1–25–29 1–21–30	INCOMPATIBILITY EXTREME. This is by far the most incompatible of the privet series. In April the leaves become yellow in the same way as the extreme cases of commercial grafts in the field. The yellowing progresses in typical fashion involving first the leaf margins and the intervenous areas. Curl, brittleness, and thickening of the leaves are very marked. By fall all the leaves have fallen. The plants do not survive the winter. The especial significance of this stock is that it duplicates in a single season the course of typical incompatibility in the *L. ovalifolium* grafts in three to seven years or more. Controls healthy. This type of incompatibility is shown in Fig. 4 (Pl. 33) which illustrates a plant of this original experiment.
Fraxinus americana	5 3	2 1	1–25–29 1–21–30	INCOMPATIBILITY COMPLETE. Of the type of the following two species but somewhat less severe. Leaves large and well developed at first (Fig. 5 of Pl. 33) but later on the summer becoming very yellow and falling. *Plants nearly dead by fall. Do not survive the winter.* Controls healthy.

Stock:	Number of grafts:	Number of ungrafted controls:	Date of grafting:	Success of graft:
Chionanthus virginica	6 3	2 1	1–25–29 1–21–30	INCOMPATIBILITY COMPLETE. Leaves very small, in little tufts at the ends of the branches, becoming yellow during the summer. *All scions dead by fall.* The symptoms, due to the greater degree of incompatibility differ somewhat from those of the privet grafts, as the leaves are never well enough developed in the beginning to exhibit the symptoms described as for *L. amurense.* Controls healthy. These symptoms are shown typically in Fig. 5 (Pl. 33).
Forsythia suspensa	5 3	2 1	1–25–29 1–21–30	INCOMPATIBILITY COMPLETE. Leaves very small, tufted at the ends of the branches, not becoming yellow but falling during the summer. *All scions dead by fall.* Incompatibility of the same type as in *Chionanthus virginica* above. Illustrated in Fig. 5 (Pl. 33). Controls healthy.

"Andenken an Ludwig Spaeth" in nearly all cases, and they were all obtained from the same parent plant.

A consideration of Table III reveals a number of interesting conclusions:

a. In the first place, it reveals a graded series of degrees of incompatibility beginning with the species *Syringa japonica* and *S. villosa*, and passing through the various species of *Ligustrum* to *L. amurense*.

b. It is further plain that the employment of *S. japonica* and *S. villosa* as understocks for varieties of *Syringa vulgaris* is questionable, while in no case is the employment of any species of *Ligustrum* justified as a lilac understock.

c. All the species of *Ligustrum* exhibit approximately the same degree of incompatibility with the exception of *L. amurense*.

d. As for *Ligustrum amurense*, the symptoms of lilac graft-blight are very striking where this species is employed as an understock. It will be remembered that in ordinary field experience the symptoms of graft-blight in Lilacs grafted upon *Ligustrum ovalifolium* do not become extreme until several years after grafting. The grafts of Lilac on *L. amurense* present a condition as though the experience with *L. ovalifolium* in six years were concentrated into a single season. The symptoms are identical with those in the field in old, very incompatible Lilacs.

e. The grafts on *L. ovalifolium* show precisely the same symptoms as distinguish privet-grafted Lilacs from own-root Lilacs in the field, the symptoms which have been watched gradually increasing to the extreme stage in incompatible grafts of Lilac.

f. The extreme incompatibility manifested by Lilac when grafted upon *Fraxinus americana*, *Forsythia suspensa*, and *Chionanthus virginica* demonstrates that the use of these species as lilac understocks is highly impractical.

It is well in this connection to compare the photographs of the lilac-on-*L. ovalifolium* graft and the lilac-on-*L. amurense* with that of the control Lilac grafted on lilac roots as indicated in Fig. 4 (Pl. 33). This brings out characteristically the differences in size of the plants, the typical symptoms of these two types of privet graft, and the striking likeness between the experimental symptoms and the symptoms in the field.

In these experiments four types of controls were employed. (a) A certain number of the stock plants of each species were permitted to grow ungrafted. These in every case remained healthy. (b) Each year there were a number of lilac-on-lilac grafts made, the number corresponding to the greatest number of grafts on any one stock species during that year. These remained healthy, and since the scions were of the same origin in both the privet grafts and the controls, the latter served as desirable checks on the development of the incompatible grafts. (c) A number of cuttings of the same parent plant as supplied the scions were rooted in the soil, and the condition of these was found to correspond in health precisely to the lilac-on-lilac grafts. (d) The parent plant of the scions served as the fourth type of control. Hence these various grafted scions were checked against sister scions grafted upon lilac roots, against the sister scions rooted directly, and against the parent tree itself. The foliage of all the controls remained identical in appearance and perfectly healthy throughout the experiments. Because of the comparative uniformity of conditions throughout these experiments and because of the employment of control plants, the appearance of the developing scions in all the grafts is taken to be directly indicative of the degree of compatibility between stock and scion.

In order to confirm the results of the grafting experiments just reported, and to compare the observations made in the Arnold Arboretum with the actual situation in nurseries, an investigation was made in 1929 of the condition of lilac plants in a number of nurseries in New England, New York, and New Jersey. The evidence forthcoming was entirely confirmatory. In the first place, it was seen that in nurseries which do not use Privet as a lilac understock there were to be found none of the symptoms of lilac graft-blight. On the other hand, in nurseries which do use Privet as a lilac understock the disease invariably occurred, and it was limited to the plants which had been propagated on Privet, even though plants propagated by other methods were in the same plots and rows as the blighted plants.

To give a still clearer conception of the correlation between privet grafting of Lilacs and graft-blight, reference should be made to my observations of graft-blight as it occurred in a typical large eastern nursery. This nursery offered a situation not unlike a well ordered experimental plot on a large scale. There were 37,000 Lilacs of all ages, and they were so grouped that each block contained plants of the same variety and age but propagated according to the different methods. The plants propagated by grafting could be distinguished from those which were not grafted by the fact that the graft unions were above the soil and so plainly in sight, while the plants grafted on lilac roots could be separated from those on privet by the fact that sufficient quantities of suckers were developed from the stock root-systems to identify the species of the stock with accuracy. In no case did a plant propagated on lilac roots show the symptoms of graft-blight. Of the plants propagated on Privet, those two years old were generally healthy, but here and there was a typically blighted plant. The three-year-old plants showed the effects of grafting to a more marked degree, which increased with the age of the plants. The effects of grafting were even more striking in those cases in which the privet-grafted plants were grown in "standard" form, that is, with a long, unbranched main stem surmounted by a compact, dense system of branches.

The type of evidence yielded by this nursery in question is best illustrated by the following descriptions of two typical plots, as transcribed directly from my field notes. Plot 1 consisted of three-year-old plants, plot 2 of five-year-old ones.

PLOT 1

"3500 Lilacs budded on Privet, 3500 budded on Lilac, side by side, under the same conditions. The two kinds of plants could be distinguished at a glance in most cases, the blighted plants being invariably on Privet and the lilac-on-lilac combinations invariably good, and in every case the word of the propagator as to stock and the occurrence of stock suckers confirmed the truth of the observation. Towards the end of the investigation, as we looked at block after block it became possible for me to distinguish immediately the stock of the plant by the appearance of the crown, and with perfect accuracy, no matter how the two kinds were intermingled."

Plot 2

"2000 budded on Lilac, 1000 budded on Privet. Neither lot was on scion roots whatsoever, the unions all being above the ground. A very distinct line could be drawn between those on lilac roots and those on privet roots. The former looked healthy, the latter distinctly yellowed, though growing side by side in the same block."

Thus it is seen that the preliminary observations made at the Arnold Arboretum, tested out under the more exacting conditions of controlled experiments, and substantiated by direct observations of graft-blight in numerous nurseries and other outdoor plantings, offer at once an explanation and the only explanation of the cause of lilac graft-blight. The mutually confirmatory evidence from all these sources leaves one no alternative but the conclusion that lilac graft-blight is due to an incompatibility which exists between lilac scions and privet stocks when united in the graft association.

E. RELATION OF GRAFT-BLIGHT TO THE DEVELOPMENT OF ADVENTITIOUS ROOTS FROM PRIVET-GRAFTED LILAC SCIONS.

As corollaries to the fact that graft-blight is due to the privet grafting method of lilac propagation, it was soon discovered (a) that there is an intimate relation between the degree of severity of graft-blight in Lilacs and the degree of development of adventitious roots from the scions of grafted plants, and (b) that this degree of development of scion roots is influenced by the technique of privet-grafting as employed in the nursery. It is pertinent at this juncture to point out in detail the reasons which have led me to these two conclusions.

As regards the relation between scion-root development and degree of incompatibility, a large number of observations were mutually confirmatory in pointing out that there is a great diversity in the amount of scion-root development in lilac-privet grafts. In some cases the scion begins to throw out adventitious roots within a year of the time of grafting. In such cases the scion soon becomes independent of the privet stock and supported by its own system of lilac roots. In other cases the scion apparently is never successful in the production of a lilac root-system. Moreover there are all degrees of scion-root development between these extremes. Figures 7, 8, and 9 illustrate cases in which there was no production of adventitious scion roots up to the time of photographing. In Fig. 3 is shown a scion-root-system of comparatively high degree of development, but still not great enough to prevent the appearance of severe graft-blight.

It is very significant that the degree of severity of graft-blight varies inversely with the ability of the scions to form their own roots soon after grafting. When scion-roots are few or wanting the symptoms of graft-blight are most severe; when, on the other hand, the lilac scions become independent of the privet root-systems soon after grafting, the symptoms are slight and the lilac scions are seen to recover from the disease. These conclusions were the outcome of numerous observations of which two examples are here given to illustrate the two important types of evidence involved.

In the first place, it was observed in the field that plants of the same age, variety, method of propagation, and external environment, differed somewhat in degree of severity of graft-blight. When such Lilacs were examined closely, it was seen that the plants displaying severest symptoms had developed fewest scion roots. Thus in one nursery a plot of plants which had been grafted on Privet in 1928 and were examined in 1929 varied in their symptoms. Those which showed marked symptoms of graft-blight had developed no lilac roots whatsoever. There were three apparently healthy plants in this plot, and on digging these up each was found to have at least fifty percent of its roots belonging to the lilac scion. A plot of Lilacs propagated in 1927 was examined, and among these, as I looked down the rows, here and there were plants which looked strong and vigorous with only slight symptoms of blight. Mingled with these in the same rows were occasional plants showing extreme blight. When the comparatively healthy plants were examined, each was found to have at least one strong lilac root, while the badly blighted plants, often growing no more than a foot away, had developed no lilac roots whatever.

A second type of evidence was obtained from a consideration of suckers from privet-grafted Lilacs. It frequently happens that a severely blighted Lilac will have attached to its root-system one or more lilac suckers which show no signs whatever of graft-blight. On dissecting the root-systems it is seen that the healthy suckers develop from adventitious buds at the base of the lilac scion, and that they draw their water and mineral salts almost exclusively from lilac roots, and not from the privet stocks of the mother plants. Hence they are economically independent of the privet stocks, and the absence of graft-blight symptoms readily yields to interpretation on this basis. A typical example of such a healthy sucker growing from the base of a severely blighted Lilac is illustrated in Fig. 3 (Pl. 32). In this figure the severe symptoms of the mother plant are strongly contrasted with the healthy condition of the sucker.

From such observations as the preceding, it was concluded that there is an inverse relation between the development of adventitious roots from privet-grafted lilac scions and the severity of graft-blight. It is essential to consider next the relation between the technique of grafting and the production of adventitious scion roots.

There are a great many variations in technique employed by lilac propagators in grafting lilac scions upon privet stocks. However, these fall into essentially three groups: topgrafting, budding, and piece-root-grafting. All three methods are extensively employed. In the case of *topgrafting* a lilac cutting is grafted above the ground upon a privet stem. This is the type of grafting illustrated in Figs. 4–6 (Pl. 33). *Budding* is similar except that instead of using a cutting of lilac as the scion, a single lilac bud is inserted into the privet stem. *Piece-root-grafting* consists in grafting a lilac cutting onto a piece of privet root and burying the union below the soil.

Almost all lilac propagators are agreed that the desideratum is a lilac upon its own roots eventually. This is claimed to follow naturally when the piece-root method is employed, and is induced in the cases of topgrafting and budding by sinking the grafted or budded plant into the soil so that the graft- or bud-union is covered by 2–12 inches of earth. The sinking of the union into the earth may follow soon upon the grafting process or may be delayed for several years. Production of adventitious roots from the scion is sometimes facilitated by scarification of the lilac scion just above the graft union.

It would be expected that such a diversity of methods would be followed by an equal diversity of degree of development of adventitious roots. Such was found to be the case. The piece-root grafting method was found to be least pernicious, the employment of this method being most favorable for scion-root development. The production of scion-roots is still further aided by planting the grafted plants so that the unions are well below the surface of the soil. With either budding or topgrafting the results are less favorable. The greatest opportunity for scion-root development is afforded if the unions are immediately buried and if the scions are scarified by a few knife cuts, just above the unions. The practice of some nurseries of so propagating their Lilacs that the unions are above the soil line when the plants are sold (two to three years after grafting) is most undesirable, because in such cases the wood of the scions is already so hard that the possibility of production of adventitious roots is greatly lessened.

Thus it is seen that although some techniques of lilac propagation by the employment of privet stocks are less pernicious than others, no method fully escapes the penalty of graft-blight, because no method assures the production of numerous adventitious roots from the scion in every case. The statements made by nurserymen who use the privet method that their Lilacs are on their own roots within a short time after grafting were found to be erroneous when such Lilacs were examined. And as a natural conclusion it follows that until a privet method of lilac propagation can be shown to produce own-root Lilacs with a high degree of success, all methods of lilac propagation which involve the use of privet stocks are to be condemned.

The foregoing concludes the discussion of the appearance and causal relation of graft-blight to the use of privet stocks. It is maintained that because of the nature of the symptoms, because of the fact that the disease could not be the result of any factor considered but the use of privet stocks in propagation, and because the disease in the field and in experimental plants shows a perfect parallel to the use of privet stocks in propagation, that the disease is the direct result of such grafting, and that its elimination can be accomplished only from the standpoint of such a conclusion. Having established this conclusion, it is of value at this point to consider the ultimate nature of the incompatibility in grafts of this type with a view to shedding light on the factors which make one graft association successful while another is incompatible.

V. NATURE OF THE LILAC-PRIVET INCOMPATIBILITY

I have spent considerable effort on inquiries into the characteristics of successful and unsuccessful graft unions and into the precise differences between lilac scions and privet stocks in an attempt to reach an explanation of the ultimate basis for the incompatibility in the lilac-privet graft. The literature on the subject of grafting yields a number of theories as to the failure of certain graft combinations. Those theories which could conceivably apply to the lilac-privet graft association are here discussed according to their merits in shedding light upon the nature of the lilac-privet incompatibility. It is manifest that the nature of graft incompatibility must in the end be referred to some fundamental difference between the protoplasms of stock and scion. Such a fundamental difference underlies the manifestation of various symptoms of uncongeniality, whether in the crown, in the root-system, or at the graft union. Hence a considerable part of this section is devoted to a report of investigations bearing on the fundamental protoplasmic differences between lilac scions and privet stocks, the problem being attacked from the standpoint of immunological experimentation.

A. ANATOMICAL UNION OF STOCK AND SCION

In a number of instances as reported in the literature, it has been found that in incompatible graft combinations the stock and scion fail to establish sufficient continuity of the conducting elements to maintain the food and water requirements of the graft components. To be sure this phenomenon is probably a manifestation of some more fundamental protoplasmic difference between stock and scion, at least in those cases in which there appear to be no anatomical differences in the wood structure of stock and scion; but as the subject has always been treated in a descriptive rather than in an experimental manner, it is of value at this point to note whether in the lilac-privet graft, as in certain other graft combinations, the symptoms developing in the crown bear any relation to an anatomical failure of stock and scion to unite.

As examples of such failures in anatomical union there may be cited several instances from the literature. Bradford and Sitton (5) found that in the incompatible grafts of Pear on Apple, and Pear on Quince the cambium continuity became broken at the end of each growing season until finally the transpiration channels and the phloem became so discontinuous that the scion failed. Waugh (36) held that failure in the incompatible unions studied was a result of the deposition of a certain amount of scar tissue between stock and scion. Proebsting (29) confirmed Waugh in finding the weakness in interspecific Pyrus grafts due to the laying down of parenchyma at the point of union, and also found that in some incompatible grafts bark tissue was present in place of this separating parenchyma. In a later paper (30) the same author added that the xylem at the line of union may degenerate into a gummy mass which might check water movement.

None of these conditions has been found to obtain in the lilac-privet graft, however. The graft failure which occurs even in ordinarily compatible graft combinations due to carelessness in the original setting of the graft (5, 6, 13, 14) was never observed in the lilac-privet graft, even though the technique was varied during the course of my experiments. Many compatible and incompatible graft unions of Lilac were examined macroscopically and microscopically. In all cases the union of the conductive and meristematic tissues was excellent after the first year. Since there is no observable anatomical difference between the woods of *Syringa* and *Ligustrum*, and since the union was perfect in practically all cases, it was impossible to distinguish under the microscope where one graft component ended and the other began. The microscopic examination failed to reveal any indication of abnormality in structure which could cause failure of the graft association. This point is illustrated in Fig. 10 (Pl. 34) which shows the microscopic anatomy of a typical incompatible lilac-privet graft union in transverse section. The original junction of the two woods shows as a line of crushed cells and a certain deposit of scar tissue. But subsequent growth was so perfect that it is quite impossible, except in a general way, to trace the dividing line between the two woods beyond the original junction.

B. RELATIVE DIFFERENCES IN THE PERIOD OF GREATEST METABOLIC ACTIVITY OF STOCK AND SCION

If the times of activity (leafing-out, blossoming, fruiting, dormancy) of stock and scion differed markedly, it might be expected that the success of the union would be jeopardized. However, there are numerous observations to show that the root systems of the plants in consideration are always potentially active and that dormancy is localized in the buds. Thus Denny and Stanton (10) have shown by forcing with chemicals that a single bud can be forced while the root is in the "dormant season," although the remainder of the lilac buds remain dormant. Likewise, observation shows that exceptionally in nature a single bud will develop in the same way. Further, if lilac plants are moved at the beginning of the dormant season, the roots begin activity, the top remaining dormant. In addition I was able to keep the crowns of lilac plants continuously in leaf throughout the whole of the dormant season by the use of chemicals and heat in forcing the dormant buds before the leaves of the current year had fallen. Moreover, in grafts made in late January of *Syringa vulgaris* on *S. villosa* (which is very late in coming into leaf) the common lilac scions had developed crowns of mature leaves and completed their season's growth a full month before the opening of the buds of the ungrafted *S. villosa* stocks. Finally, in a graft of common Lilac upon *S. villosa* in which the scion was accidentally broken off soon after it had commenced growth, the buds of the *S. villosa* stock commenced development, due to the stimulus of the abortive grafting process, a month before the buds of the other ungrafted *S. villosa* stocks began to develop. All these observations point to one fact: Dormancy is localized in and conditioned by the buds. The absorbing and conducting systems are potentially active twelve months of the year. Hence, if these facts be applied to the graft union, it will be seen that it is immaterial whether the root-system belongs to a plant which is normally "early" or "late." If the root-system is capable of activity at all times, the scion will determine and control the absorption and conduction of the raw materials of the soil.

C. RELATIVE RESISTANCE OF THE VARIOUS STOCKS TO DISEASE

In a number of instances the Privet has shown itself susceptible to certain diseases and insects which may exert an unfavorable influence on the graft union. Among these may be mentioned the privet borer, the crown gall disease caused by *Bacterium tumefaciens*, which I have found on the privet roots of a number of grafted commercial Lilacs, and possibly the privet anthracnose caused by *Glomerella cingulata.* A typical crown gall from the privet roots of a commercial Lilac is illustrated in Fig. 7 (Pl. 34). None of these diseases bears sufficiently consistent relation to the lilac disease, however, to merit consideration as the cause of the lilac graft-blight, serving rather merely as complicating features.

D. RELATIVE HARDINESS OF THE LILAC SCION AND THE PRIVET STOCK

California Privet has been anathematized as an understock for Lilac by northern growers (9) since it is not reliably hardy much north of New York City. Doubtless such growers are justified in their opinion, but south of New York I have observed the customary symptoms of graft-blight, and even in Boston it is only exceptionally that California Privet is root-killed in the winter, in spite of the fact that graft-blight occurs in mild years. The northern growers have an additional reason, but not an exclusive one for condemning the practice of grafting Lilac on Privet.

E. RELATIVE VIGOR OF THE LILAC SCION AND THE PRIVET STOCK

A number of observations seem to point to the fact that an imporant factor in the ultimate failure of lilac grafts on Privet is the inability of the privet roots to cope with the water requirements of the growing lilac scion. From the facts that the symptoms are those of chronic water deficiency, that the privet grafts thrive at first and do not show the disease in its extreme form for several years, and that actual examination of the root-systems of blighted plants shows obvious gross insufficiency in root development for the size of the crown, it is concluded that herein lies an important factor in the failure of the lilac-on-privet grafts.

That this insufficiency of the privet system is related to the inability of certain substances to cross the graft union is seen in the large swelling due to accumulated food just above the graft union, not only in the lilac graft but in numerous grafts of other plants, as for example the grafts of Navel or Valencia Oranges or Eureka or Lisbon Lemons upon *Citrus aurantium.* Webber (37) considered this characteristic of certain graft unions of considerable importance in determining the congeniality of graft unions; and that this is a constant character in the lilac grafts is seen from an examination of the figures of lilac root-systems at the end of this paper.

F. SPECIFIC PHYSICO-CHEMICAL OR IMMUNOLOGICAL DIFFERENCES BETWEEN STOCK AND SCION

This is a province which I approach with a considerable degree of hesitation, as it is not strictly within the field of the pathologist, and is, moreover, most controversial and obscure. We are profoundly ignorant of the ultimate physiology and physical chemistry of the interreactions of living protoplasms. That the relative vigor of stock and scion is not the only factor involved in the failure of lilac-on-privet grafts is shown by the early symptoms and death of the grafts of *Syringa vulgaris* on *Ligustrum amurense*, as well as by the incompatibility of Lilac and *Chionanthus*, *Forsythia*, and *Fraxinus*. In the precise nature of the physiological basis for this incompatibility we have a question which cannot yet be answered by the biological sciences. But in an attempt to draw a little nearer to an understanding of a possible immunological basis for graft incompatibility, I have attempted a number of experiments with the Lilac, and should mention them, although it is impossible, before a great deal of fundamental investigation has been accomplished, to draw many definite conclusions.

Plant immunology is nearly a virgin field in striking contrast to the high degree of development of animal immunology. The first real impetus to the science came as a sequent to Osborne's monumental work in isolating plant proteins (27). Such pure plant proteins, as well as crude plant-protein-containing mixtures were used in inoculating animals, a line of work which has been carried out in a number of laboratories in America and Europe. Mez and his followers using this technique have built up a complicated phylogenetic system based on this reaction (22, 23, 24). The fact that Mez's results are deemed somewhat questionable by other European and American workers has led to a bitter controversy on the continent, with the result that the subject of plant immunology is held to be rather fruitless by many present day investigators. In all this work, however, the *plant* was secondary in consideration. It was an animal which furnished the reactions observed, and it is essential to distinguish here the difference between immunological reactions in which plant proteins are the stimulus to induced immunization in an animal, and the reactions in which the plant itself is the organism developing the power of protection against foreign proteins by means of precipitation, cleavage, or other method of removal from activity of the foreign protein. The former reactions belong properly to the domain of animal immunology, the latter constitute plant immunology in its proper sense.

When one considers the essential similarity in vital processes between animal and plant protoplasms it is a natural corollary to expect a like relation with regard to the ability of the organism to protect itself by means of immunological mechanisms. The more conservative of the animal immunologists are inclined to doubt the practical possibility of demonstrating such a similarity, giving as their reasons the absence in the plant of a conductive system comparable to the blood system of the higher animals, the difficulty of obtaining plant proteins in pure condition, and the relatively great dilution of plant protein in extracts made by the customary procedures in comparison to the high concentration of animal protein in blood serum. Granting all these difficulties, it is nevertheless entirely possible to obtain comparable reactions by choice of suitable techniques, and since the plant does possess certain advantages in comparison to animals, such as ease of cytological investigation, the field of plant immunology in its restricted sense is worthy of serious consideration in the light of possible explanations of heretofore obscure biological processes within the plants.

The pioneer work in plant immunology consisted in an attempted application of the techniques and theories of animal immunology directly to plants without essential modification. For example, plants were infected with pathogenic bacteria and the extracts subsequently made were tested for their agglutinative and lytic properties against the bacteria in question. The outcome of these endeavors has not been very satisfactory because of the limited application of the animal methods. Most of this work was done in the laboratories of southern Europe, and although it is beyond the scope of this paper to deal with this phase of immunology in plants, an excellent account of the whole subject and literature is to be found in the "Immunità nelle piante" of Carbone and Arnaudi in 1930 (7). To the literature should be added mention of a paper by East and Weston (12) in 1925 in which the hypothesis is advanced that in Sugar-cane the plants "may gain a temporary immunity after an experience with mosaic similar to that a human being attains after recovering from a virulent typhoid infection." All of these experiments, observations, and hypotheses are based on the conception that in plants there may be a display of immunological phenomena analogous to that due to the mechanisms of immunity in animals.

A most valuable forward step in plant immunology was the elaboration of this conception of immunological mechanisms in plants by Kostoff working in East's laboratory in 1928 and 1929 (17, 18).

A new technique was developed, that of grafting species of Solanaceae and investigating the possibility of acquired immunity as a result of such graft unions. From one point of view, the graft union is a case of parasitism of scion on stock, this parasitism being somewhat reciprocal, however, as each biont provides something to the economy of the complex. But the essential feature here is that in the graft union we have a most intimate association of plants of distinctly different species in which the opportunities for mutual sensitization and immunization are far in excess of those in the other methods of plant immunology heretofore investigated. Kostoff tested leaf extracts of stock and scion before grafting and periodically after grafting. Not only were normal antibodies found in the Solanaceae, but it was found that after grafting in many cases there was an acquirement or increase of immunity as demonstrated by precipitin and lysin reactions. These antibodies were sometimes specific, sometimes not so. One of the most striking bits of evidence offered was that after grafting the reaction of leaves just above the graft union was greater than that of leaves farther removed from the place of union, that is, the precipitating potency spread outward from the graft union to the more distant parts of the plant.

Using this work as a starting point, I performed more than a thousand precipitin and lysin reactions in the Oleaceae with especial reference to the grafts of Lilac on Privet. The results of these experiments are introduced here, not because they offer a final answer to the question of graft incompatibility of the type under consideration, as the whole field is yet too young to permit of dogmatism, but rather in order that they may shed some light upon the matter of plant immunology and serve, in conjunction with other data which shall be forthcoming in the future, to help in laying the foundations of plant immunology as an experimental science.

Since I was dealing with woody plants in distinction to the herbaceous Solanaceae, and since the term of life, rapidity of growth, age of flowering, and annual cycle of foliation and defoliation are so different in the Oleaceae, it was necessary to modify somewhat the technique previously employed. Briefly my procedure was as follows. From five to twenty-five grams of leaves were collected from each of the plants to be investigated. The leaves were cut from the plants, when turgid, with a sterile razor. (*Note:* Chemical sterility rather than biological sterility is indicated throughout this section wherever the word "sterile" is employed.) The leaves of each plant were washed in tap water, rinsed in sterile water, dried between sterile cotton, and weighed immediately. They were then cut up in small pieces with sterile scissors and ground in a sterile unglazed porcelain mortar until in a thick paste with no fragment more than one millimeter in diameter. The paste was then placed in a sterile test-tube of suitable size and with it was mixed twice the weight of the leaves of distilled water which was first used to rinse out the mortar and pestle. The test-tube was immediately stoppered with sterile cotton and placed in a refrigerator for 24 hours at 2° C. At the expiration of this time, the mixture in the tube was filtered until the filtrate was crystal clear. Even slight opalescence was eliminated by repeated filtration. For filtering it was sometimes possible to attain the results desired by means of one or two passages through ordinary, fairly fine filter papers. (The finer, hard, thin, Schleicher & Schüll papers proved most satisfactory.) In more refractory cases it was necessary to use other means, as the quantity of extract was necessarily so small as to cause absorption of the liquid by the paper to detract seriously from the quantity of liquid. Hence, where it was necessary to filter more than twice, an apparatus was used which reduced the absorption to .1 cc. per filtration. This apparatus consisted of a sterile Gooch crucible with a filtering disc of finely divided Jena glass. (The No. 4 of Arthur Thomas Co. proved most serviceable.) This crucible fitted into a sterile thistle-tube and was rendered air-tight by a thick rubber collar. The lower end of the thistle-tube extended through a 1-hole rubber stopper into a filter-flask, and was so arranged that the filtrate dropped into a sterile three-inch test-tube within the filter-flask. The filter-flask was attached to a suction pump. The material to be filtered was placed in the Gooch crucible and the filter-flask evacuated. Even under these circumstances filtration was sometimes very slow, but a clear liquid usually resulted after one or sometimes two or three passages through the filter. After filtration the liquids were clear, varying in color from lemon-yellow to dark amber, and strongly acid. The tubes were immediately placed in a beaker of water surrounded by a bath of melting ice, and used in testing.

In the testing, from .2 to .4 cc. of the liquid of greater specific gravity was introduced into specially made sterile test-tubes measuring 30 mm. in length and with an internal diameter of 2–3 mm. by means of a pipette of exceedingly fine bore at the tip. The second liquid (of lower specific gravity) was so pipetted into the same tube as to form a clear layer over the first, separated from the first by a very thin refractive plane. This required a good deal of care in order to avoid mixing the two. The specific gravity was determined by trial and error each time, as the appearance of an extract gave no clue to its density. In a negative test this layering remained unchanged for one hour or longer. In a positive precipitin test, after one minute to fifteen minutes (usually about three to five minutes), the refractive zone became a very thin cloudy zone (Uhlenhuth's ring). This cloudiness increased in intensity and the zone became thicker and thicker until it was milk-white and about 2-3 mm. thick. Then from its lower margin little white rootlike projections would begin to penetrate the clear lower extract in tortuous paths. More of these would form and grow longer, until finally the whole of the lower two thirds of the contents of the tube became milk-white and all signs of layering were lost. The whole process generally took about forty minutes. The test-tubes were held in a rack devised by riveting little bent strips of brass to a brass rod in such a way that the spring of the brass clips would hold the tubes firmly in place. Observation was made in doubtful cases by viewing through a large lens with obliquely transmitted light against a black background. The refraction of the walls of the test-tubes was eliminated where necessary by immersing the test-tubes in a small plane-sided vessel of cedar oil. But in good reactions (indicated by "2" to "4" in the tables below) the Uhlenhuth ring was so plain, even in these small test-tubes, as to be visible at a distance of several yards. Notes on each reaction were taken at intervals of 1, 5, 10, 20, 30, and 40 minutes and longer where there was any doubt, while full details of the origin and constitution of the plants and extracts were kept in every case.

The small tubes and pipettes were cleaned by boiling for two hours in .5% sodium carbonate solution and then for four hours in four changes of distilled water. This was followed by washing in two changes of alcohol and one of ether. The larger glassware was washed in water and then in alcohol and ether. The Gooch crucibles were cleaned by flushing through with alcohol and ether and then burning to whiteness over a Bunsen flame.

The various features of this technique were tested out in detail during the course of these investigations. Extracts were preserved by placing in the refrigerator at 2° C and covering with a fairly thick layer of toluene. In such cases they were found to retain their potency for at least several days as a rule. But for the most part the experiments reported below were performed with fresh extracts. The results are indicated under the heads of NORMAL REACTIONS and REACTIONS OF BLIGHTED PLANTS. By the former is meant reactions in which the extracts were made from healthy, ungrafted plants.

Normal Reactions

The precipitin tests made in the Oleaceae show that there are no normal precipitins present in the genera of the Oleaceae studied that are demonstrable by the technique employed. A table of these tests follows (Table IV). The proper names in all cases refer to the horticultural varieties of *Syringa vulgaris*. "*Ligustrum vulgare*" here includes both the species and the variety *foliosum*. "*L. obtusifolium*" includes the variety *Regelianum*. Otherwise no varieties were employed except as specified. In this and the other data given below, the following symbols are used:

– : No reaction.
t : Trace or doubtful reaction.
1 : Weak but definite reaction.
2 : Moderate reaction.
3 : Strong reaction.
4 : Maximum reaction.
0 : Lytic reaction. (Formation of a clearer zone separating the two extracts. Of doubtful significance at present.)

TABLE IV. NORMAL PRECIPITIN REACTIONS IN THE OLEACEAE.

	Chionanthus virginica	Fraxinus americana	Forsythia suspensa	Ligustrum acuminatum	L.amurense	L.ibolium	L.ibota	L.macrocarpum	L.obtusifolium	L.ovalifolium	L.vulgare	Syringa japonica	S.vulgaris	" Aline Mocqueris	" Amethyst	" Arthur W. Paul	" Edmond Boissier	" Gigantea	" Languis	" Ludwig Spàth	" Marie Legraye	" Maurice de Vilmorin	" Michel Buchner	" Mireille	" Mme.Casimir Përier	" Mme.Lemoine	" Près.Carnot	" Princesse Marie	" Spectabilis	" Verschaffeltii
Chionanthus virginica	-	-			-					-										-										
Fraxinus americana	-				-					-										-										
Forsythia suspensa																				-										
Ligustrum acuminatum					-	-		-	-	-	o		-	-				-			-		-		-	o	-	o		
L.amurense	-	-		-		-	-	-	-	-	-	-	-					-			-		-		-					
L.ibolium				-	-		-	-	-	-	-		-				-			-			-		-	-		o		
L.ibota				-	-				-	-	-				-	-	-		-	-		-		-					-	-
L.macrocarpum			-	-	-			-	-	-		-	-	-							-		-		-					
L.obtusifolium				-	-	-	-	-		-	-		-	-	-	-	-	t	-	-	-	-	-	-	-	-	-	o	-	-
L.ovalifolium	-	-		-	-	-	-	-	-		-	-	-				-			-										
L.vulgare				o	-	-	-		-	-					-	-	-	t	-	-		-		-	-	1	-	o	-	-
Syringa japonica					-					-										-										
S.vulgaris				-	-	-		-	-	-																				
" Aline Mocqueris				-				-	-												-									
" Amethyst							-		-		-																			
" Arthur W.Paul							-		-		-						-													
" Edmond Boissier					-	-	-		-	-	-					-				-										
" Gigantea				-					t		t																-	o		
" Languis							-		-		-																			
" Ludwig Spàth	-	-	-		-	-	-		-	-	-	-					-			-										
" Marie Legraye				-				-	-					-																
" Maurice de Vilmorin							-		-		-																			
" Michel Buchner				-	-	-		-	-																					
" Mireille							-		-		-																			
" Mme.Casimir Përier				-	-	-		-	-		-																			
" Mme.Lemoine				o		-			-		t																	-		
" Près.Carnot				-					-		-						-											o		
" Princesse Marie				o		o			o		o							o								-	o			
" Spectabilis							-		-		-																			
" Verschaffeltii							-		-		-																			

An examination of the data presented above reveals at once the striking difference between the Solanaceae and the Oleaceae. In the former family Kostoff found many examples of normal immunity. Here, on the other hand, is a manifest absence of such immunity. This lack of positive reactions cannot be attributed to the technique as the tests indicated were performed with the same extracts as gave the positive reactions to be seen in the next table. In no case, in the combinations of species and varieties considered, was there even a moderate reaction; in one case we find a weak reaction; and there are a few borderline cases. In a few instances there appears to be a lytic zone formed at the junction of the two extracts; but this is not consistent, is weak, and is apparently of no great significance. A number of these reactions were repeated several times, the rest once. This absence of positive reactions with normal extracts is all the more striking in view of the high precipitin potency of extracts from diseased Lilacs.

REACTIONS OF BLIGHTED PLANTS

In contrast to the above normal reactions, a similar series of tests of grafted lilac scions against the various stocks was made simultaneously. The results are seen in Table V below. In no case was the "blighted" extract taken from any but a plant suffering from graft-blight. Experiments with Lilacs suffering from blights due to other causes will be considered subsequently. In every case the following scheme of controls was employed:

Immune lilac extract	+ normal privet.	Normal lilac	+ normal privet.
"	+ " lilac.	" "	+ " lilac.
"	+ other immune lilac extracts	" privet	+ " privet.
"	+ distilled water.	" "	+ distilled water.
		" lilac	+ " "

In conjunction with Table IV, the data in Table V are very suggestive. It will be seen that in the first place, in every one of the plants suffering from graft-blight there is a strong acquired precipitin potency. This varies in intensity from plant to plant as would be expected where some of the plants are suffering from the disease to a greater extent than others. But in every case there is a marked development of this property. The precipitin potency is, moreover, not specifically directed against one species of *Ligustrum* or against all Privet species, since a definite, although weaker, reaction exists between the privet-grafted Lilac and the normal Lilac as well as between two specimens of privet-grafted Lilac. In addition it is seen that the reactions are appreciably stronger in general against some of the Privet species, weaker against others. Thus the lilac

TABLE V. PRECIPITIN REACTIONS OF GRAFT-BLIGHTED LILACS.

		Lilac grafted on privet, showing the blight:																				
		Archeveque	Arthur W. Paul	Belle de Nancy	Caroli X	de Jussieu	Gen.Haig	Gen.Kitchener	Henri Simon	Hermann Eilers	Hugo Koster	Hyazinthenflieder	Jules Simon	Lavoisier	Leopold II	Mme.Lemoine	Messemaker	Michel Buchner	Roi Albert	Rubra de Marly	Souv.de Rothpletz	Violacea
Normal privet	Ligustrum acuminatum							1	3		1	4	3	2				4			-	4
	L. amurense							-	2		-	1	2					1			t	3
	L. ibolium								3		-	2	1			1		3		1		
	L. ibota		4	4		4				4						4	4		4	2		
	L. macrocarpum								3			4	2					3				4
	L. obtusifolium		3	4		4		4	4	4	4	4	3	4		3	3	3	4	1	-	4
	L. ovalifolium	3					-				-				-	t				-		
	L. vulgare	-	4	4	t	4	3	4	4	4	4		4	4	3	4	4		4	-	t	
Normal lilac	Aline Mocqueris																	2				
	Amethyst																-					
	Andenken an L. Spath		2								-											
	Arthur W. Paul		2	2													1					
	Edmond Boissier		3													4				t		
	Languis																t					
	Marie Legraye																	3				
	Maurice de Vilmorin																		2			
	Mireille																1					
	Mme. Casimir Perier												3									
	Mme. Lemoine							1			-			1							-	
	Princesse Marie							1			-			t							-	
	Spectabilis																		2			
	Verschaffeltii																		3			
Graft-blighted lilac	Belle de Nancy					2				3												
	Caroli X																o					
	de Jussieu			2						2												
	Gen. Kitchener										-			1							1	
	Henri Simon												1									
	Hermann Eilers			3		2																
	Hugo Koster							-			t			1			1				2	
	Jules Simon								1													
	Lavoisier							1			1										3	
	Messemaker				o						1											
	Rubra de Marly															-						
	Souv. de Rothpletz							1			2			3								

extract is strongly precipitated by *Ligustrum vulgare*, *L. obtusifolium*, and *L. ibota*, while the weakest reaction is against *L. amurense* and *L. ovalifolium*. The difference in reaction against *L. amurense* is in accordance with the fact that *L. amurense* is manifestly different from the other *Ligustrum* species in its graft reactions. But *L. ovalifolium* is the understock generally used throughout these lilac grafts, and if the precipitin reaction were a specific antibody-antigen reaction in the graft of *Syringa vulgaris* on *Ligustrum ovalifolium* it would be expected that the greatest reaction would be obtained against this species of Privet.

It is significant in this same connection that the acquired precipitins in the grafted Lilac are potent against ungrafted healthy Lilac, although this potency is somewhat weaker than against Privet. The reactions of grafted Lilac against ungrafted Lilac are typical and indistinguishable from those of grafted Lilac plus Privet, with the only exception that they are somewhat weaker in general. The reactions of grafted Lilac against grafted Lilac seem to bear some relation to degree of severity of the blight. That is, a severely blighted Lilac tests strongly against a mildly blighted Lilac, less strongly against a severely blighted plant in general.

The reaction was consistently uniform if repeated from beginning to end. The variations found in such repetitions were insignificant. This fact not only served as a valuable check on minor variations in technique, but likewise strengthened the whole significance of the reactions. For example, the following tables give examples of five

TABLE VI. NORMAL PRECIPITINS

Normal precipitin reaction of *Syringa vulgaris* v. "E. Boissier"—Normal
Tested against *Ligustrum vulgare*—Normal

Date:	Potency of reaction after: 1 min.	5 min.	10 min.	20 min.	30 min.	40 min.
8-30-29	—	—	—	—	—	—
9-1-29	—	—	—	—	—	—
9-3-29	—	—	—	—	—	—
9-5-29	—	—	—	—	—	—
9-7-29	—	—	—	—	—	—

TABLE VII. ACQUIRED PRECIPITINS

Acquired precipitin reaction of *Syringa vulgaris* v. "E. Boissier"—Blighted
Tested against *Ligustrum vulgare*—Normal

Date:	Potency of reaction after: 1 min.	5 min.	10 min.	20 min.	30 min.	40 min.
8-30-29	—	1	2	3	4	4
9-1-29	—	1	2	3	4	4
9-3-29	t	1	2	3	4	4
9-5-29	t	1	2	3	4	4
9-7-29	t	1	2	3	4	4

repetitions of the same experiment, each separately performed from beginning to end on successive days. The test was a healthy Lilac and a typically blighted Lilac of the same variety and clon against the *same* extracts of *Ligustrum vulgare*. The data show only slight fluctuations in the readings at the end of the first minute, and this is due to the rapidity of appearance of the reaction and the relative difficulty in deciding between no reaction (–) and a trace of a reaction (t).

It is to be noted that in the preceding discussion I have frequently used the word "blighted" rather than "grafted" when referring to Lilacs suffering from graft-blight. The reason for this is that in the first place no positive test was ever forthcoming from a grafted Lilac unless it showed moderate to extreme symptoms of graft-blight (yellowing, leaf-curl, leaf-thickening, etc.). During the course of development of the graft-blight symptoms of my experimental grafts of Lilac on *Ligustrum amurense* and *L. ovalifolium* I performed weekly precipitin tests from the time the leaves appeared until the time the symptoms were extreme. The positive precipitin test appeared only when the leaves began to show the acute symptoms mentioned above (136 days after grafting). In the second place the term "blighted" is used because it was found during these studies that the positive test is obtained when the precipitating extract comes from a plant showing symptoms similar to graft-blight, even though the plant has never been grafted. For example, certain types of soil and root deficiency, boring of the canes by Lepidopterous larvae, drought, and various types of local injury produce symptoms sometimes resembling those of graft-blight. And in some of these cases strong positive precipitin tests were obtained, differing in no wise from the tests of Lilacs suffering from acute graft-blight. A few such tests are indicated below:

1. The Lilac "Edmond Boissier," in the preceding table (Table VII) had a history of having been propagated by cuttings in 1921. It was, however, suffering from an unfavorable environment. During the very dry summer of 1929 the leaves became yellow (although the plant recovered the following, moister summer) and the plant resembled in some measure plants suffering from graft-blight. The tests were positive as is seen from the above table. Further tests with the same plant were:

		Tested against normal:
S. vulg. "E. Boissier" (Blighted)	4	*Ligustrum vulgare*
" " "	3	*L. obtusifolium*
" " "	4	*L. ibota*
" " "	3	*Syringa vulg.* "E. Boissier"
" " "	1–3	" " (other varieties)

2. *Syringa vulgaris* "Michel Buchner." This plant was claimed by the propagator to have been propagated from cuttings. It was suffering from acute drought, there having been no rainfall whatever

for nearly six months in the locality from which it had been obtained, as in the Lilac "Edmond Boissier" above. Its reactions were all "4" against *Ligustrum vulgare*, *L. obtusifolium*, and *L. ibota*.

3. *Syringa vulgaris* "Ranunculiflora" from the same source as No. 2 above and suffering from drought with similar though milder symptoms was negative to the same three Privet species. This was also true of a wild seedling of *Syringa vulgaris* from the same nursery.

4. Another plant, *Syringa vulgaris* "Deuil d'Émile Gallé," similar in symptoms and environment to No. 1 above although suffering from the drought to less extent, gave the following reactions:

		Tested against:
S. vulgaris "Emile Gallé" (Blighted)	t	*Ligustrum amurense*
" " "	2	*L. acuminatum*
" " "	—	*L. ibolium*
" " "	t	*L. macrocarpum*
" " "	2	*L. obtusifolium*
" " "	3	*L. vulgare*
" " "	— to 1	Normal Lilac
" " "	—	Blighted Lilac

5. *Syringa vulgaris* "Mme. Casimir Périer." The plant was in perfect health except for one branch which was notably chlorotic from the depredations of a cane borer. The blighted branch and a healthy branch *of the same plant* were tested with the following results:

(a)		Tested against normal:		(b)
Lilac "Périer"	—	*L. vulgare* (Leaves)	3	Lilac "Périer"
(Healthy branch)	—	*L. vulgare* (Fruit)	2	(Blighted branch)
" "	—	*L. obtusifolium*	3	" "
" "	—	*L. macrocarpum*	t	" "
" "	—	*L. ibolium*	t	" "
" "	—	*L. acuminatum*	3	" "
" "	—	*L. amurense*	1	" "

6. *Syringa vulgaris* "Louis Henry" was similarly blighted from a root-rotting disease, although according to the records it had not been grafted. Its reactions were:

		Tested against normal:
S. vulgaris "Louis Henry" (Blighted)	4	*L. vulgare* (Leaves)
" " "	3	*L. vulgare* (Fruit)
" " "	4	*L. obtusifolium*
" " "	t	*L. macrocarpum*
" " "	1	*L. ibolium*
" " "	2	*L. acuminatum*
" " "	t	*L. amurense*

7. The reactions of three own-root plants suffering from local root injury and displaying chlorotic symptoms were tested by using both healthy and chlorotic branches from the same plants respectively, with the following results:

		Tested against normal:		
(a) Lilac "Gigantea" Local injury	—	*L. vulgare*	t	(a′) Lilac "Gigantea" Healthy Same plant as (a)
	—	*L. obtusifolium*	t	
	—	*L. acuminatum*	—	
(b) Lilac "Prés. Carnot" Local injury	4	*L. vulgare*	—	(b′) Lilac "Prés. Carnot" Healthy Same plant as (b)
	4	*L. obtusifolium*	—	
	2	*L. acuminatum*	—	
(c) Lilac "Prin. Marie" Local injury	1	*L. vulgare*	0	(c′) Lilac "Prin. Marie" Healthy Same plant as (c)
	—	*L. obtusifolium*	0	
	—	*L. acuminatum*	0	

Thus it is seen from all these examples that the precipitin potency is not an inseparable sequel to the ill effects of grafting, since it may be brought about by purely abiotic factors. In this respect its specificity is seriously thrown open to question. This is all the more striking in contrast to the precise specificity of animal immunology. Apparently the degeneration in the leaf tissue is of such a nature as to alter the precipitating power of the extract derived therefrom, but attractive as is the hypothesis that this is a direct and inseparable reaction of the lilac protein and the privet protein analogous to the reactions of mammalian blood to foreign proteins, one can hardly hold to such an hypothesis in view of the results seen above.

The physical and chemical properties of the extracts were investigated to a limited extent with the following results:

1. The precipitating power of the extracts is independent of the pH of the extracts within very wide limits. This is in conformity with Kostoffs' findings (l. c.) as well as those of animal immunologists (20).

2. Heating of the antigenic extract (normal Privet) momentarily to any temperature between 0° C and 90° C does not destroy the precipitating power if the extract be used immediately. Heating of the antibody extract (blighted Lilac) momentarily to any temperature between 0° C and 100° C does not destroy the power of the extract of being precipitated if the extract be used immediately. This is not in accordance with the situation in animal immunology where the sera are relatively sensitive to heating and where the precipitating powers are usually destroyed long before 90° or 100° C is reached.

3. The reaction is similar, though a little weaker, if 10% NaCl solution is used as a solvent of the antigen rather than distilled water.

4. In one experiment, boiling, acidification, and filtration of the resulting precipitate did not lessen the precipitating potency of the antibody extract of graft-blighted Lilac.

5. The extracts automatically precipitate themselves if kept at room temperature in from a few hours to several days. The antibody extracts autoprecipitate very easily, the antigenic extracts less easily. This proved to be one of the greatest technical difficulties in the work.

6. The proteins of the leaf extracts differ from animal proteins in a number of ways as was first pointed out by Osborne (27). Thus they are hydrolized by .3% NaOH, are densely precipitated by the addition of 20% alcohol, and do not precipitate strongly when treated with weak acids.

7. It may be remarked parenthetically that as a by-product of this work with extracts it was found that oospores of the lilac fungus *Phytophthora Syringae* are produced abundantly in sterile lilac leaf extracts, although their production is difficult in many cases by the use of the ordinary techniques.

In addition to the precipitin experiments outlined above, I also performed a series of lytic tests, working on the theory that even though the mixture of two protein extracts did not result in visible precipitates, yet there might be a disruption of the foreign protein molecule into various cleavage products which might be demonstrated by a suitable technique. This type of defensive reaction is found in animals, and it would not be extraordinary to find its homologue in plants.

As a reagent I used Ninhydrin (Triketohydrindene hydrate) (1, 32) in a 1% aquatic solution. This is a test for a number of protein cleavage products. Its delicacy is so great that in my preliminary tests I was able to get a positive test with peptone in a dilution of 1:50,000. However, as far as I went with the use of this reagent, my results were negative. This does not necessarily mean either that the technique is not applicable here or that there is no lytic disintegration of the foreign protein molecule, as the scope of my work on this head was not sufficiently extensive to warrant such conclusions.

A consideration of the foregoing data leads one to a choice of two interpretations. Either (a) the reactions manifested by the extracts of the Oleaceae represent purely physical phenomena and are independent of any specific immunological property, or (b) we have here true immunological phenomena but differing markedly from the phenomena of animal immunology. The facts that the reactions are non-specific and that the precipitin reaction may be reproduced in all detail by purely physical means are evidence for a physical interpretation of the reactions. On the other hand, they are independent of both pH and concentration of extracts, which would not be expected if they were purely physical. Alternately, the reactions may be truly immunological. The protein molecule of the healthy plant has undergone a certain decomposition in the degenerative processes exhibited in the blighted plants considered, and it is conceivable that under such conditions the resulting cleavage products might possess immunological properties different from those of the original protein molecule from which they have been derived. Yet if the reactions are truly immunological they are certainly radically different from the phenomena of animal immunology, as witness the reactions of plants blighted because of external environmental factors.

It is not possible at present to decide definitely which of the two alternatives is applicable here, nor to dogmatize upon the subject. However, this much may be said. The great differences in the circumstances attending the reactions from those in animal reactions (as impurity of the extracts, different types of proteins, relatively great dilution of proteins, greater sensitivity of the animal as made possible by the circulation of the blood) are sufficient to cause one to expect a somewhat different display of immunological phenomena. As yet the technique is crude. One deals with an extract of varying concentration and chemical constitution, an extract which is a conglomeration of many substances, probably of constantly fluctuating composition. It is rather surprising that one does obtain consistent results under these conditions.

From the evidence with regard to immunological phenomena in the Oleaceae as outlined in the preceding pages, a number of conclusions may be drawn:

1. The technique of plant immunology, with certain modifications, is shown to be applicable to a study of the lilac-privet graft.

2. Normal precipitins are not demonstrable within the species of Oleaceae considered and according to the technique employed.

3. Strong acquired precipitins are found in the leaves of Lilacs suffering from severe typical graft-blight.

4. The acquired precipitins show little specificity within the limits of these experiments.

5. Analogous or identical reactions may be obtained from the leaves of Lilacs suffering from blight due to other causes. This fact offers an hitherto uncontrolled source of error in plant immunology as investigated along these lines.

6. Neither normal nor acquired lysins were demonstrated in the Oleaceae, although the possibilities in this field have by no means been exhausted.

7. The grafting of Lilac upon Privet results in symptoms of disease in the crown and also results in pronounced changes in the immunological properties of the leaf-extracts. The precise nature of the relation between these phenomena is not yet understood, because of a lack of fundamental knowledge of the exact limits and nature of the precipitin reaction.

8. The immunological technique is not diagnostic of graft-blight, but it is diagnostic of a type of crown disease which may be due to a number of causes, including incompatible grafting.

9. The application of plant immunological technique to a study of the normal and morbid physiology of plant tissues would probably be fruitful in the light of these experiments.

VI. PRESENT STATUS OF LILAC PROPAGATION

Having determined the cause of graft-blight it was next desirable to take up the subject of the control of the disease. However, in order to accomplish this end most effectively, it was of value first to make a brief survey of the present status of the lilac industry in America and Europe. The purposes of the survey were to determine how Lilacs are being propagated, why they are so propagated, the state of mind of the growers with regard to lilac propagation, and the economic situation with regard to the lilac industry.

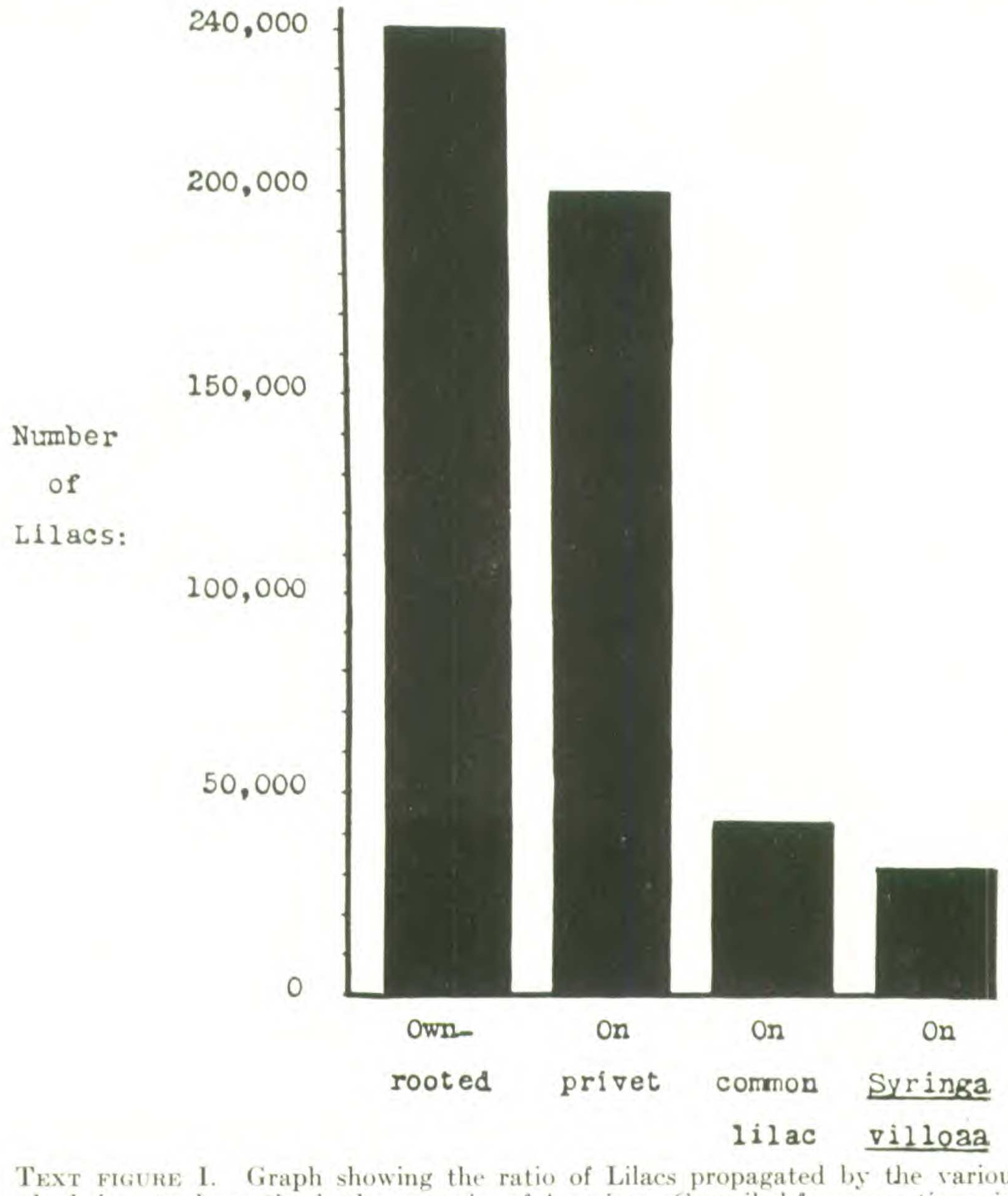
With these purposes in mind, a questionnaire was sent to all the important lilac propagators and experts in the United States, as well as to a number of the leading, representative growers in Canada and Europe. The results exceeded all expectations. Complete replies were received from fifty-two of them. These fifty-two propagators are at present engaged in the growing of nearly a million lilac plants. That they comprise a representative cross section of the lilac industry in America and Europe is seen from their distribution, which is as follows:

United States: Cal. 1; Col. 1; Conn. 1; D. C. 1; Ga. 1; Ill. 3; Mass. 6; Mich. 2; Minn. 1; N. J. 4; N. Y. 6; Ohio 2; Ore. 1; Pa. 4; Tenn. 1; Vt. 1; Wash. 1	37
Canada	2
England	5
France	1
Germany	2
Holland	4
Switzerland	1
	52

The most significant questions proposed in the questionnaire were: (1) What are the methods of propagation practiced by you in growing Lilacs? (2) What success has been attained in the various methods practiced? (3) How much time is required to produce a two-foot plant by the methods employed? (4) What is the retail price at which a two-foot plant must be sold to afford a reasonable profit? (5) What methods of propagation have you found undesirable and why? (6) What is your opinion with regard to own-rooted versus privet-rooted Lilacs? (7) If you use Privet as an understock, how long does it take for the plants to get on their own roots, in general? (8) Have you observed any weakness or diseased condition in Lilacs which you think might be traceable to the method of propagation? (9) If cost were not a factor, how would you propagate lilacs? (10) Approximately how many Lilacs have you in all stages of cultivation? The answers to these questions brought out several striking and hitherto unknown facts with regard to the lilac industry.

It is to be borne in mind that in this, as in all similar collections of data, one must appreciatively weigh the opinions of the correspondents on unproved matters. However, with regard to some details, the data can be accepted without reserve, as for example those matters of actual practice in vogue, and of cost of production. The replies to the questions asked of the nurserymen are considered at this point.

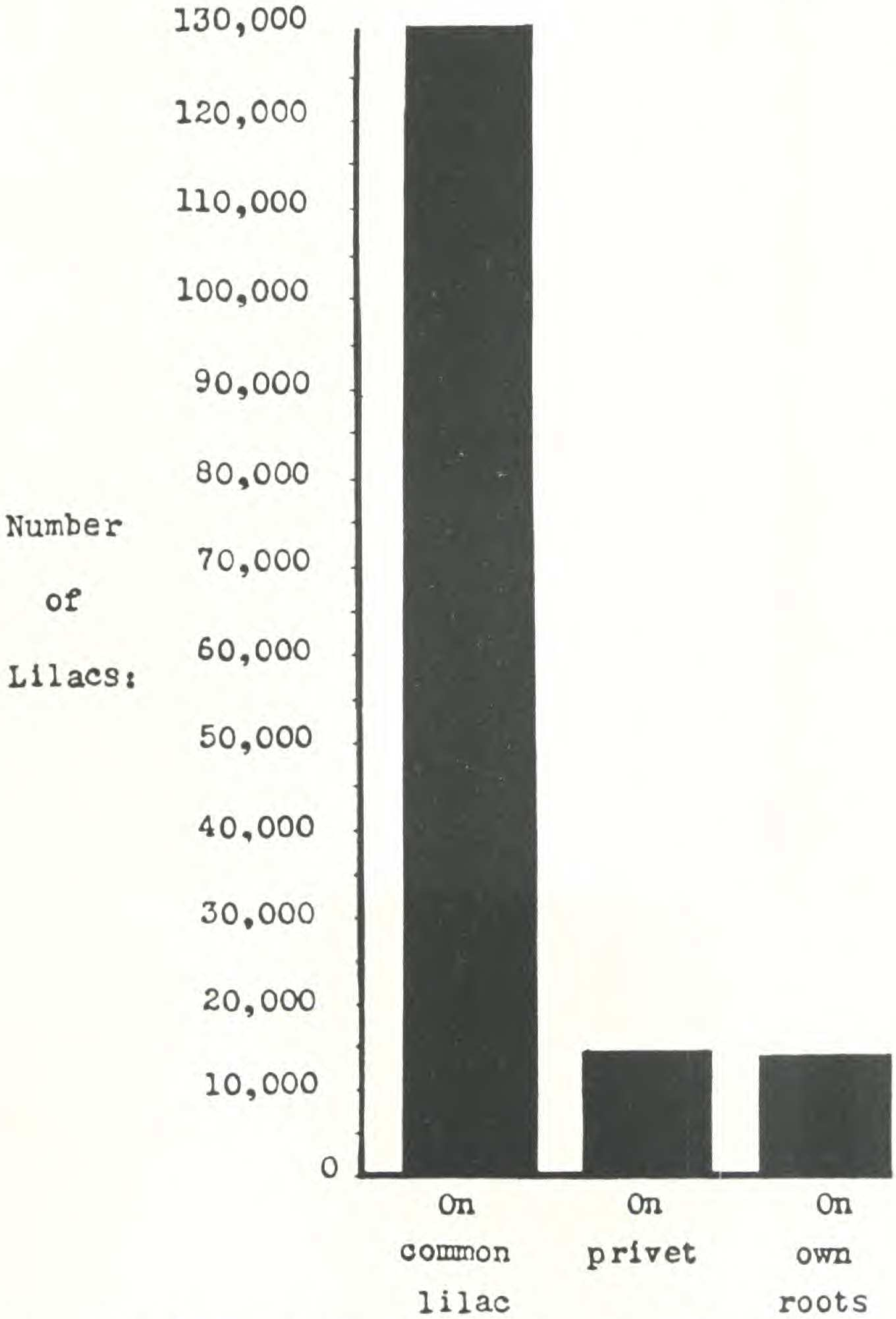
It was necessary to know at the outset what methods of lilac propagation are actually being employed today. It was found that in the United States Lilacs are being propagated commercially by a large number of methods with each method capable of numerous modifications. Lilacs are being propagated by various own-root methods comprising rearing from seed, suckers, layers, hard-wood cuttings, and soft-wood or green-wood cuttings, and in contrast to these methods by budding, piece-root grafting, and top-grafting on the various stocks: *Syringa vulgaris*, *S. villosa*, *Ligustrum ovalifolium*, *L. ibota*, *L. sinense*, *L. vulgare*, and *L. ibolium*. Growing Lilacs from seed is limited for the most part to the "pure" species of Lilacs, as the named varieties do not come true from seed. Propagation by suckers and layering is very limited, being employed only on a very small scale because of the large number of parent plants required. The use of hard- and green-wood cuttings is very extensive, the details of the practice differing, however, with individual propagators. All these methods give own-root plants in which the questions of incompatibility and the suckering of the foreign rootstock do not enter. Nurserymen are divided in their opinion as to the desirability of joining a lilac crown with a foreign root. Budding is economical of the wood of the named variety; top-grafting is easily done at a time when the nurseryman is relatively free of other duties and rapidly produces good-sized plants; root-grafting gives the minimum assistance from the foreign root-system, and hence is least pernicious from the standpoint of incompatibility. As is seen, the stocks employed vary widely. Of all these methods, however, the three outstanding types of lilac propagation are: (1) propagation by own-root methods (which involves almost entirely



TEXT FIGURE 1. Graph showing the ratio of Lilacs propagated by the various methods in actual practice in the nurseries of America. Compiled from questionnaire data.

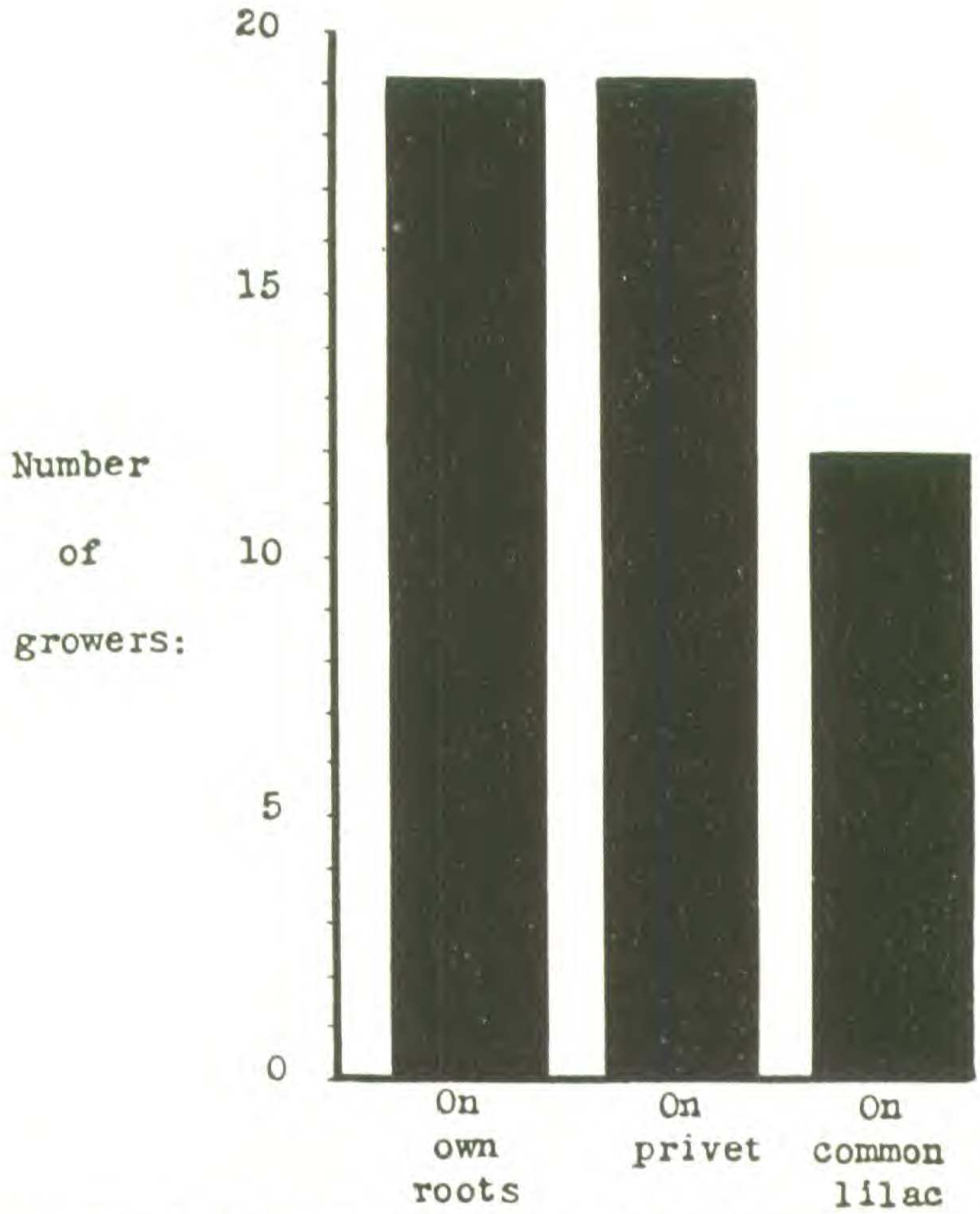
the use of cuttings), (2) propagation by budding, top-grafting, or root-grafting onto some species of Privet, generally *Ligustrum ovalifolium*, and (3) propagation by budding, top-grafting, or root-grafting onto the common Lilac, *Syringa vulgaris*.

These three main types of propagation indicated are employed in the United States according to the proportions represented in the graph in Text figure I. The proportions will appear very surprising to many who are acquainted with the lilac industry, since it is a common belief among lilac fanciers that the majority of Lilacs in this country are grown on privet roots. But since the questionnaire



Text figure II. Methods of lilac propagation employed in Europe. The striking difference between this and the preceding figure is explained in the text. Compiled from questionnaire data.

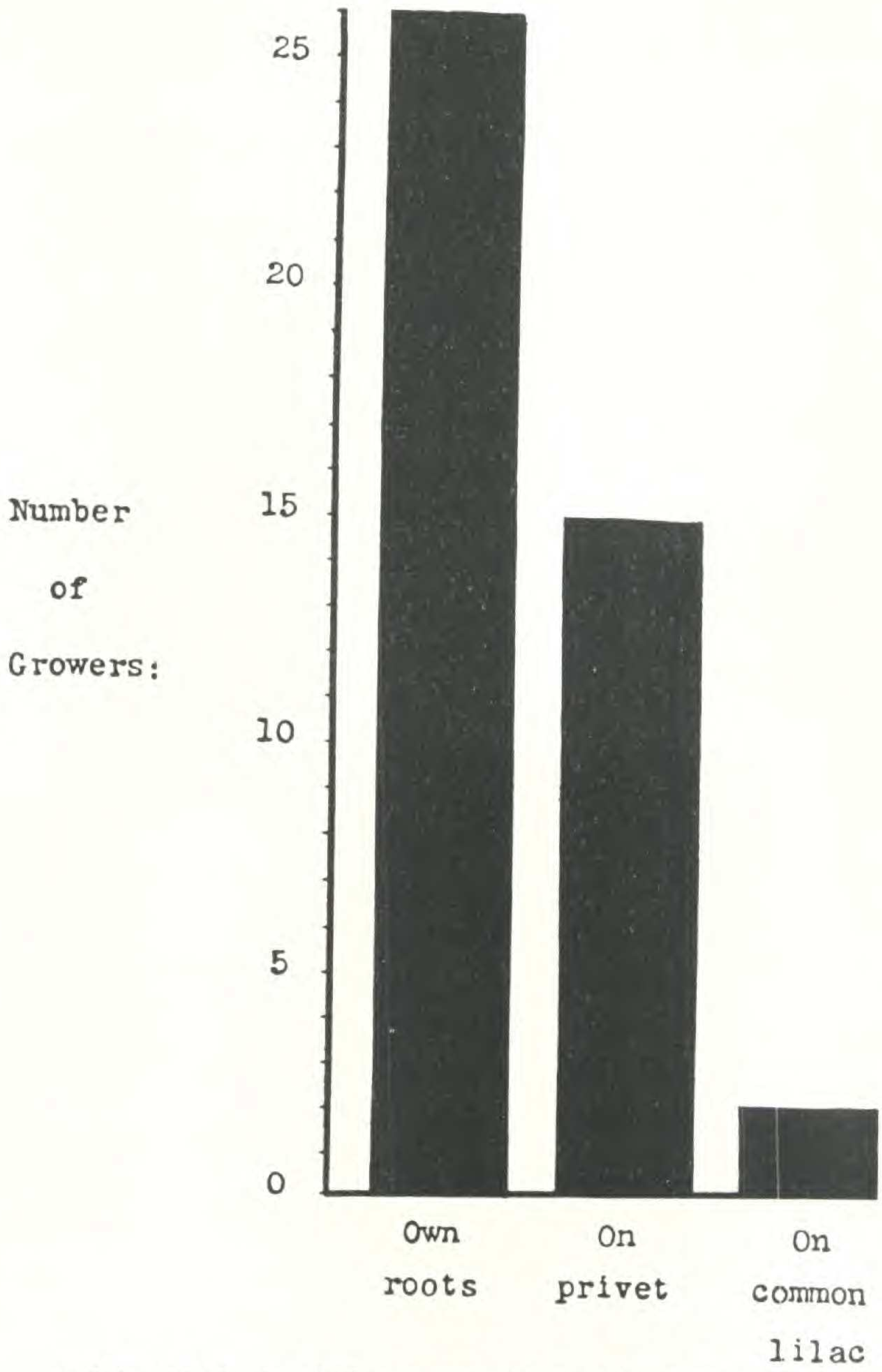
is of such scope as to be representative of the lilac industry in America, the results are incontestable. The essential point to be drawn from the graph is that there are at least as many Lilacs grown in America by own-root methods as on Privet. This fact stands in distinct opposition to statements found in the horticultural literature, such as, "American nurserymen are now almost universally using California Privet (as a lilac understock)" (39, p. 34), and "growing Lilacs from cuttings has been almost discontinued except in a very few nurseries" (39, p. 33). The data presented likewise show incontrovertibly that lilac propagation by own-root methods (that is, by the use of cuttings) is commercially practicable, since it is already employed on a large scale under existing conditions.



TEXT FIGURE III. Methods of lilac propagation actually employed in America and Europe today. Compare with the following graph. The difference in the graphs of Text figures III and IV represents a body of nurserymen who recognize the superiority of own-root Lilacs but are unable to produce them because of the competition with those growers who insist on using the cheaper privet method.

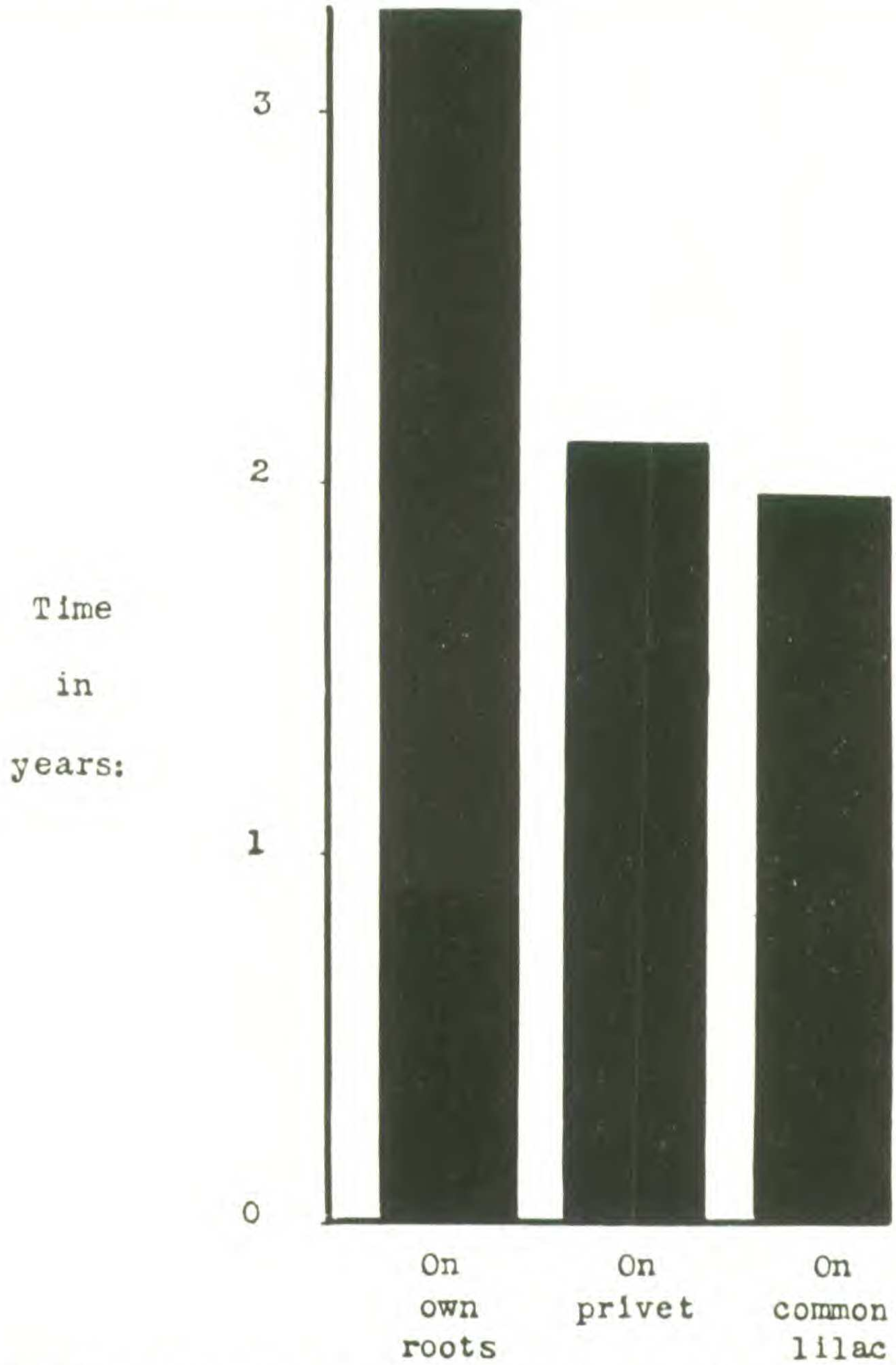
In Europe the situation is somewhat different, since the commerce in cut blossoms assumes greater proportions and the requisite is speed in production of blossoms, and not necessarily long-lived plants. Forcing the Lilac by heat, chemicals, etc., is extensively employed, and hence it has been found that propagation by means of grafting or budding onto the common Lilac fulfills the requirements in the majority of cases. The actual situation in Europe is shown in Text figure II.

The reason for the employment of Privet as a lilac understock is an economic one, as is quite apparent from a study of the data presented in Text figures III and IV. Text figure III represents the actual prevailing situation with regard to the number of propagators using the various methods of propagation considered. Text figure



TEXT FIGURE IV. Methods of lilac propagation which would be employed by the propagators of America if it were not for the additional expense of propagation on own roots.

IV, on the other hand, represents the relative number of propagators who would use the respective methods were it not presumably impossible for them to leave out of consideration the fact that own-root propagation is slower and more expensive. It will be seen from a comparison of the two graphs that there is a considerable number of propagators who are using Privet as a lilac understock because they are forced to by the economic stress of competing with producers who use the cheaper privet method. These propagators would turn to own-root methods if they could afford it, since they recognize the superiority of the own-root plant. On the other hand,

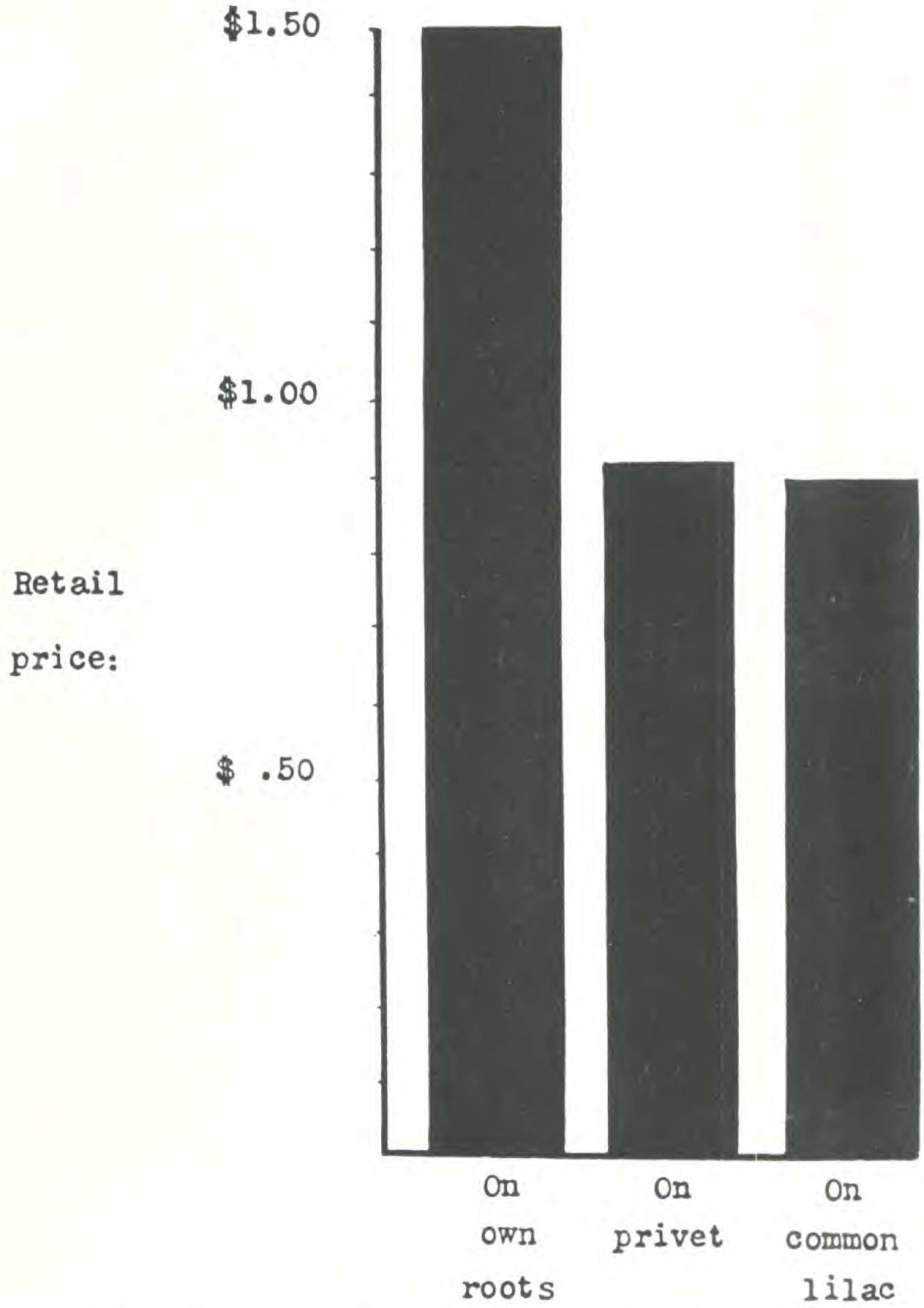


TEXT FIGURE V. Relative time required to produce a two-foot lilac plant by the methods of propagation indicated. Compiled from questionnaire data. Discussion in the text.

there is a certain body of nurserymen who fail to perceive the superiority of the own-root Lilac, and are content with the privet method.

A measure of the greater cost of growing Lilacs by own-root methods is afforded by a consideration of Text figures V and VI.

Text figure V gives the actual ages of marketable Lilacs as grown by the various methods of propagation. It will be seen that the own-root Lilac is in the nursery about a year longer than the grafted Lilac. If this be translated into dollars and cents (Text figure VI) it will be seen that the own-root Lilac costs about sixty cents per plant more than the grafted Lilac, the sixty cents representing the



TEXT FIGURE VI. Relative cost of production of a two-foot lilac plant propagated according to the methods indicated. Compiled from questionnaire data. Discussion in the text.

additional year of care in the nursery. It will be noted that Text-figures V and VI are almost superposable, which indicates the intimate relation between speed of production and cost of production.

Turning now to the question of the percentage of success of Lilacs as propagated by the various methods, we find the experience of the nurserymen rather at variance. In budding or grafting, whether on lilac roots or on Privet, most propagators obtain from 80% to 100% of saleable plants from the original number of plants budded or grafted, the percentage being fairly uniform. But with respect to the use of cuttings, the results are hardly so consistent. In general those nurseries which propagate by cuttings on a large scale show creditable percentages of plants from the number of cuttings planted in the soil. Those which use the method as an alternative or in a small way often report rather low percentages. Some of these percentages are given to illustrate this point.

Reported percentages of saleable plants:

Softwood cuttings:—0–75; 20–40; 25; 49; 50; 50; 60–75; 65; 72; 75; 75; 75–100; 80; 80; 89; 90; 100; 100.
Hardwood cuttings:—15; 15; 25; 40; 75; 90; 100.

Some propagators find that one type of cuttings is desirable, the other wholly undesirable. In part this is due to equipment, because bottom heat in the greenhouse bench is an almost necessary adjunct to the rooting of lilac cuttings. But it is sufficient to say that the rooting of cuttings by one means or another can be accomplished with a high degree of success, and is being done by a number of large nurseries. Since this is so, failure in the rooting of cuttings is due to faulty technique on the part of the operator and does not justify condemnation of own-root methods of lilac propagation.

It is very apparent to one who has dealt with this question that the method of propagation of Lilacs is an open and live problem to nurserymen. Opinions are at variance, and accordingly it was to be expected that in a survey such as was carried out in connection with this study a great many contradictory statements should be obtained. Such was the case. It would be interesting to include here some of the various remarks on both sides of this question which have been received in correspondence; but space forbids such an inclusion. In lieu of this I can only state that many of the nurserymen are cognizant of a weakness in lilac plants resulting from the privet-grafting procedure. Many others feel that the lilac-privet graft is a desirable method of lilac propagation if and only if the Lilac is able to produce a scion root-system. Almost no propagator will argue that a Lilac is satisfactory unless it does produce scion roots, although many experienced nurserymen contend that the grafted plant does get on its own roots, and adhere to the privet method because of its relative apparent economy in comparison with own-root methods. Bearing this in mind, the following section will deal with an analysis of the desirable and the undesirable points of the various methods of lilac propagation in order to give a background for the recommendations for the control of lilac graft-blight.

VII. CONTROL OF LILAC GRAFT-BLIGHT

The legitimate evidence for and against the various ways of propagating Lilacs as gleaned from the questionnaire as well as from my own observations and experiments is here briefly stated:

A. PROPAGATION BY BUDDING OR GRAFTING ON COMMON LILAC

For the production of ornamental shrubs, the practice of grafting or budding upon common Lilac is undesirable. Opinion is nearly unanimous among nurserymen that under such conditions the danger of suckers from the grafted rootstock is so great as to eliminate this method from consideration. To the amateur these suckers are indistinguishable from the named variety. They soon devitalize the scion and completely choke out the named variety. This method does have the advantages of being rapid, cheap, and offering perfect compatibility, and is practical in those cases in which the Lilacs do not leave the hands of trained nurserymen, as in the forcing industry of Europe, but under American conditions the sucker nuisance is sufficient to outweigh any of the advantages of the method.

B. BUDDING OR GRAFTING ON SPECIES OF SYRINGA OTHER THAN S. VULGARIS

In some cases it is evident from my grafting experiments indicated in section IV, that a relatively moderate incompatibility exists between the common Lilac and the other Lilac species. Until a Syringa stock is proven to be compatible and at the same time shown to be either free from the sucker habit or producing suckers which can be easily recognized as such, until such a stock is found and is obtainable in sufficient quantity, the species of Syringa may be eliminated from consideration as understocks for Lilacs. *Syringa villosa* is claimed to have been used successfully for this purpose; but according to my experience with this stock it is rather questionable whether its use is justified in view of the moderate degree of incompatibility manifested by grafts of *S. vulgaris* on *S. villosa*. *Syringa japonica* falls into the same category.

C. BUDDING OR GRAFTING ON FRAXINUS, CHIONANTHUS, AND FORSYTHIA

Fraxinus, *Chionanthus*, and *Forsythia* have proven to be so completely incompatible with Lilac as to eliminate them from consideration as lilac understocks.

D. BUDDING OR GRAFTING ON LIGUSTRUM SPECIES

No species of *Ligustrum* has been shown to be more compatible with Lilac than *L. ovalifolium*. Hence the elimination of *L. ovalifolium* on the grounds of incompatibility automatically eliminates all the other species of Privet considered in this paper. The use of Privet has the advantages of being very rapid, hence cheaper, of requiring less skill than propagation by the use of cuttings, and of being more conservative of the wood of the plant supplying the scions. It has a number of disadvantages as compared with own-root methods, which more than offset the advantages. Chief among these is a greater or less incompatibility, resulting in shorter life of the scion, weaker growth, and unsuitability for forcing. In addition to this there are the disadvantages of the tendency on the part of the privet stock to sucker, its relative susceptibility to cold, and its susceptibility to certain parasites, such as the crown-gall bacterium and the privet borer. Finally, in some cases at least, it has been found that the union of Lilac and Privet results in a graft association which is mechanically weak and easily broken by accident.

If the lilac scion rapidly threw out roots after it had been grafted on Privet, it would soon become independent of the privet stock. Such does happen in some cases, but very frequently no attempt is made by the scion to root itself, at least until years after the grafting procedure. The statements that Lilac grafted on Privet are on their own roots within two or three years are erroneous, being founded on untested opinion. This question was included in the lilac questionnaire and the replies were far from uniform. Individual estimates ranged from "one year" to "never," and almost no two propagators agreed as to the length of time consumed before the grafted Lilac is independent of the privet stock.

Many lilac root-systems were examined in the course of this study. These showed that only in exceptional cases is the lilac root-system well developed soon after grafting. An examination of the root-systems of one shipment of thirty-three typical Lilacs from a nursery which claims that its Lilacs are on their own roots within two years after grafting on Privet, showed well over half still almost completely dependent on the privet stock at the end of this time. Compare Figures 7 and 8 (Pl. 34) in this respect, which illustrate two representative Lilacs from this particular shipment.

As a matter of fact there are great differences in the technique of grafting and the method employed exerts a definite influence on the matter of scion-root formation. Thus one nursery which buds Lilac onto Privet never brings the scions nearer than two inches above the soil before the Lilacs are sold. The consumer is instructed to bury the Lilacs considerably deeper than they stood formerly. Such Lilacs are very slow in forming scion roots and exhibit a high incidence of graft-blight. In other cases the budding or grafting is above ground but the Lilacs are progressively buried deeper until the scions lie well below the surface. Chances for own-rooting are greater here, although there is still a high incidence of graft-blight. Finally some propagators merely graft a small piece of a privet root to the scion and plunge the whole into the soil. This method is least pernicious of all, but does not completely eliminate the blight.

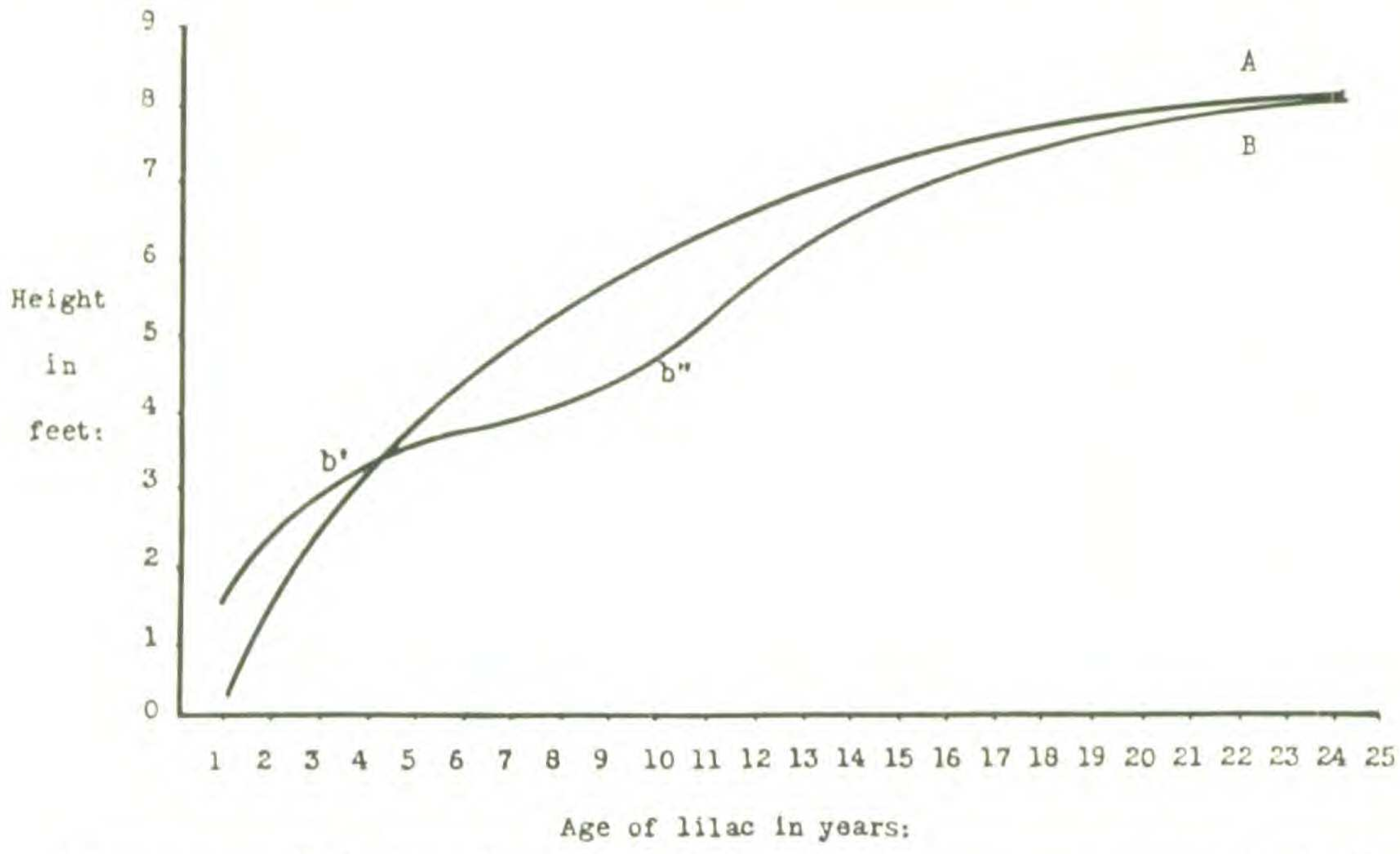
The essential point is that no matter what care be taken to induce the scions to form their own roots, they do not always do so, and *even in the most carefully handled privet-grafted plants, the incidence of graft-blight is sufficiently high to prohibit the use of Privet in lilac propagation in any form hitherto employed.*

I say "in any form hitherto employed" because it is conceivable that the privet method might be so modified as to be safe, although this would involve a little care on the parts of both the propagator and the consumer. This could be accomplished by some method which would eliminate the privet root bodily after it had served its purpose of carrying the Lilac over to the point where it had started to form its own roots. Two methods of doing this are suggested: (a) The propagator could feel sure of the future health of his plants, as far as graft-blight is concerned, if he would clip away the old privet rootstocks completely before the plants are sold. The crowns would have to be cut back proportionally, and this method could only be used when the scions had started root-formation. Since the own-rooted plant from cuttings is not much slower in getting started than the privet-rooted plant if the latter must be cut back severely, this plan might not show much advantage over the own-root methods. (b) The other method suggested is as yet theoretical but worthy of trial. If at the time of propagation the graft union be bound with wire, firmly but not too tightly, then as the plant grew the privet root would become automatically cut off. The Lilac would be forced either to form scion roots or to perish. This is an alternative worthy of serious consideration by those who insist on using Privet in lilac propagation, but it has not been proven as yet.

E. PROPAGATION BY THE USE OF HARD- AND SOFT-WOOD CUTTINGS

This method has the disadvantages of being slower and hence more expensive, of requiring greater skill, and of taking more "mother wood" for the production of a given number of plants. It has the advantages of absolute freedom from incompatibility, resulting in longer life and better, stronger plants. There is never danger of suckers from a foreign rootstock choking out the plant or of confusing the named variety with the rootstock variety. It is practical. With care a high percentage of plants can be obtained. In the Arnold Arboretum during the past few years successful propagation by cuttings has been employed with fifteen species of *Syringa* and more than one hundred varieties of *S. vulgaris*. Of all the varieties of *S. vulgaris* in which the method was employed, 95.2% were rooted successfully from cuttings. Hence there is no justification for the omission of the use of cuttings in lilac propagation on the grounds that it is impractical or unsuccessful.

In answer to the chief argument advanced against the use of own-root methods, namely that the growth of own-root plants is relatively very slow as compared with that of grafted plants, it is desirable at this point to take up the matter of comparative rapidity of growth of grafted and own-root Lilacs in some detail.



TEXT FIGURE VII. Growth curves of Lilac propagated by own-root methods (A) and by budding or grafting on Privet (B). Curves constructed from measurements of more than 500 Lilacs of all ages during the years 1928–1930. Curve B does not represent the growth of individual plants but rather the totality of growth of many grafted plants. Discussion in the text.

It is self evident that Lilacs grown from cuttings are slower in getting a start than budded or grafted plants. Wister (39) represents this same situation in graphical form. But it has been pointed out earlier in this paper that sooner or later there is a checking effect in many of the privet-grafted plants. This fact has occasioned the question: Do the own-root Lilacs ever equal or surpass the privet-rooted Lilacs? The answer to this question is found in Text figure VII, which represents the normal growth curve of Lilac plants propagated on own roots as compared with the growth curve of privet-rooted Lilacs. It is seen that at the age of two or three years, the normal selling time for lilac plants, the grafted plant is about a foot taller than the own-root plant. But as the privet-rooted plant reaches the age of three or four years the graft-blight begins to manifest itself. Numerous plants fail to make any growth at all. And the result as shown by the figure is that the own-rooted Lilacs attain the same size as the grafted plants in approximately four to five years on the average. From this time forth until maturity the own-root plants are larger and in every way superior to plants which have been propagated on Privet. From the fifth to the tenth years many of the privet-rooted plants die out, many others are culled out as being unworthy of further care, while some recover from the blight. The result of all these factors is to cause the privet-graft curve to rise again, till at maturity the two kinds of plants are indistinguishable, although there has been a heavy mortality in the privet-grafted plants. It must always be borne in mind that isolated plants may not follow this curve. Some grafted plants soon form scion-root systems and follow the normal curve. Many others never reach maturity. The technique of grafting or budding has an effect which has already been considered. But the significant fact to gain from these data is that *in general the own-root plant does overtake the privet-rooted plant, and surpasses it in size and desirability.* The time at which the own-root Lilac overtakes the privet-rooted plant is not until after the plants have left the hands of the producer and are in the garden of the consumer. This fact in no way lessens the responsibility of the nurseryman, whose interest ideally lies in his plants throughout their entire life, yet it tends to obscure the importance of the root-constitution of his Lilacs since the extreme symptoms are not seen in the nursery by the propagator but in the private planting by the purchaser.

F. RECOMMENDATIONS

Having analyzed the various methods of lilac propagation, it seems fitting to close this paper with the following recommendations for the control of the lilac graft-blight:

1. Own-root methods of lilac propagation are unhesitatingly recommended as being unquestionably sound, practical, and in the long run economical.

2. Propagation on *Syringa vulgaris* rootstocks is not considered justified because of the sucker difficulty, at least under American conditions.

3. The use of Privet as a lilac understock should be abandoned unless a method is adopted, such as has been suggested, which will eliminate the privet root-system before the plant is sold.

4. If the consumer can be led to see the desirability of own-root plants, and if the producer will look beyond the immediate present and have regard for the welfare of his Lilacs after they leave his hands, then the consumer will be willing to pay the slightly higher price for his own-root plants, and the producer will not tolerate the production of any but permanent plants. Hence an important feature of any program of elimination of the lilac graft-blight is the education of the consumer to demand permanent plants and of the nurseryman to produce them.

VIII. SUMMARY

1. The present paper describes an unrecorded and destructive disease of the common Lilac, *Syringa vulgaris*, to which I have given the name "Graft-blight" of Lilac.

2. The disease is found to be widespread throughout the United States and of sufficient severity to occasion the loss of many thousands of prized Lilacs every year.

3. The symptoms are those of general nutritional deficiency, characterized by a progressive yellowing of the leaf margins and intervenous spaces, reduction in the size and number of the leaves, brittleness and curling of the leaves, premature or abnormally late leaf fall, and the resulting stunting of the growth of the plant as a whole. Since the effects are cumulative from year to year, the possibility of recovery is very limited.

4. The disease is proved to be independent in its causation of any parasitic organism or contagious principle. It is likewise shown to be relatively independent of the external environment.

5. The use of Privet (*Ligustrum* species) as a grafting understock is demonstrated to be the cause of the symptoms indicated. This conclusion is reached through an extensive observation of Lilacs in the field as well as through the reproduction of the disease in carefully controlled experiments. The symptoms are found to be precisely correlated with the use of certain species of privet understocks in propagation.

6. The chief undesirable factor in the lilac-privet graft is considered to be a discrepancy in the vigor of growth of the two graft symbionts which is caused or aided by the interruption of elaborated substances in their passage from the crown to the root-system, although that there are other physiological factors involved is apparent from a consideration of the experimental results.

7. In an attempt to shed some light on the problem of graft incompatibility in the Lilac, the precipitin technique was applied to the lilac-privet graft. The methods and experimental results are described in detail. A total absence of normal precipitins was found in the Oleaceae. Graft-blighted plants exhibited a high precipitin potency which, however, was non-specific within the limits of this study. A possible explanation of this lack of specificity is advanced. Although the subject of plant immunology is still so problematical as to render definite conclusions difficult, these experiments serve their purposes of extending the field of plant immunology by focussing attention on a hitherto unconsidered variable—the state of health of the tissues involved, and of the development of the precipitin reaction as related to morbidity of the plant cell.

8. By means of a questionnaire submitted to most of the leading lilac growers in America and some in Europe, it was possible to determine with accuracy the present status of lilac propagation with regard to such points as present methods of propagation, their relative desirability, and relative cost of production of Lilacs according to the various methods of propagation employed.

9. On the basis of a comparative analysis of the possible methods of lilac propagation, a number of recommendations for the elimination of lilac graft-blight have been made. These recommendations include the abolishment of the use of Lilac as understock, the discontinuance or modification of the use of Privet in this capacity, the encouragement of the use of own-root methods, and the education of the consumer and the producer as to the greater desirability of own-root Lilacs.

IX. ACKNOWLEDGMENTS

The investigation reported in this paper centered in the laboratory, greenhouses, and outdoor plantings of the Arnold Arboretum. I am grateful to Professor J. H. Faull for direction and encouragement throughout the entire investigation. I am also under obligation to Dr. E. H. Wilson, late Keeper of the Arnold Arboretum, for numerous suggestions, to Professor E. M. East for suggestions with respect to the immunological experimentation, to Mr. Wm. Judd for technical assistance in lilac propagation, and to the lilac propagators who made possible the compilation of data regarding the present status of the lilac industry.

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January 8, 1931.

EXPLANATION OF PLATES 31 TO 34

Fig. 1. Healthy Lilac, variety "Leon Matthieu," seven years of age. An own-rooted plant for comparison with Fig. 2.

Fig. 2. Lilac of the variety "Arthur William Paul," aged seven years. A typical and severe case of graft-blight. In contrast with Fig. 1, this plant is grafted on privet roots. In every other respect the plant has received similar treatment to the plant shown in the preceding figure.

Fig. 3. *Syringa vulgaris* variety "Hugo Koster." This plant was grafted on privet in 1925. The photograph shows it suffering from severe, typical graft-blight in 1930. The line through the root-system approximately divides the privet stock roots from the lilac scion roots. The one healthy shoot is a sucker from the lilac root-system. This sucker shows no sign of the blight, since it is practically independent of the privet root for support.

Fig. 4. Left to right: *Syringa vulgaris* grafted upon *S. vulgaris;* the same grafted upon *Ligustrum ovalifolium;* the same grafted upon *Ligustrum amurense.* These are typical plants from the grafting experiments reported in Section IV. The photograph was taken five months after grafting and shows the normal condition of the lilac-on-lilac graft, the moderate symptoms of the graft of Lilac upon California Privet, and the extreme symptoms of the graft of Lilac upon Amur Privet.

Fig. 5. Left to right: *Syringa vulgaris* grafted upon *S. japonica* (control); the same grafted upon *Forsythia suspensa;* the same grafted upon *Fraxinus americana;* the same grafted upon *Chionanthus virginica.* Typical appearance of these graft combinations four months after grafting. Further explanation in the text.

Fig. 6. *Syringa vulgaris* variety "Rubra de Marly" grafted upon *S. vulgaris.* The scion was taken from a plant showing extreme graft-blight as in Fig. 3. Illustrating the complete recovery of the scion due to the substitution of a lilac root-system for the privet root-system of the parent plant.

Fig. 7. *Syringa vulgaris* variety "Boule Azurée," root-system. A commercial plant at selling time, two years after grafting upon Privet. The scion has formed no lilac roots, and the plant is in addition handicapped by the presence of a crown gall in the privet root system.

Fig. 8. Another plant of the same source as that shown in the preceding figure. The crown was just beginning to manifest the extreme symptoms of graft-blight. Note the swelling at the graft union, the absence of scion roots, and the obvious inadequacy of the privet root-system.

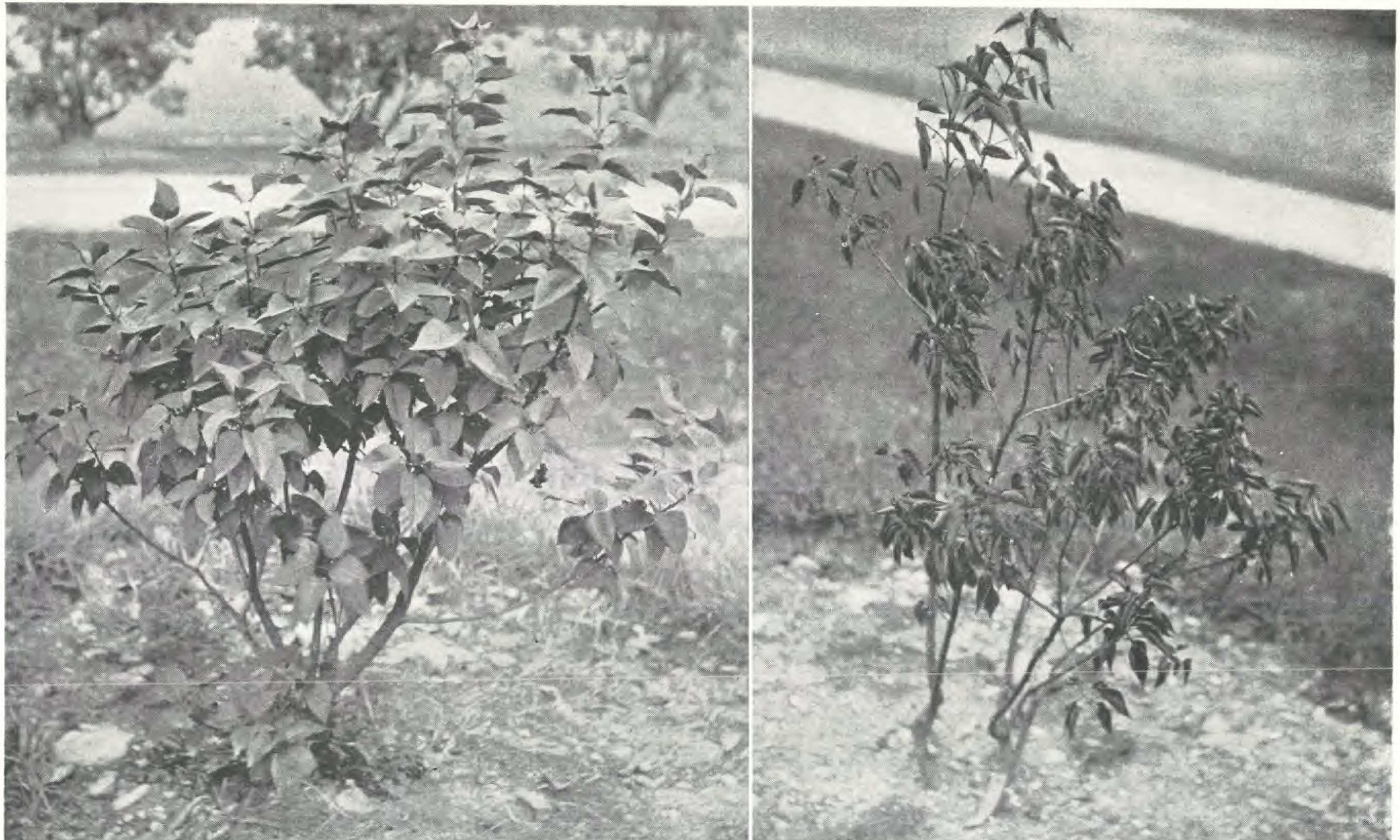
Fig. 9. Root-systems of two lilac plants which died from graft-blight. Neither had made any attempt at scion-root formation. These were commercial plants which had been retained in a private collection for several years after purchase and given ample opportunity for establishment on own roots.

Fig. 10. Photomicrograph of a typical graft union of Lilac and Privet. The broken line abc represents the original junction of the cut surfaces and is marked by crushed and irregular cell structure. At c the cambiums of stock and scion fused completely, so that thenceforward, approximately to d, it is impossible to trace the line of demarkation.

NOTES

Species of Rhododendron.[1]—Under this title the Rhododendron Society has issued a volume containing descriptions of all the known species of the genus with the exception of those from New Guinea, Malaya and Indo-China. About 700 species of which 33 are new are described, arranged under more than 40 series, some of them divided into subseries. The arrangement of the series and of the species under each series and subseries is alphabetical, but under each series a key to the species is given, so that it will be possible to identify an unknown species, if one recognizes the series. A representative species of each series and subseries is illustrated usually by a full page text figure of a flowering branch with analyses. The descriptions are as complete as possible and each is printed on a separate page which will make it feasible to arrange the species and series in any desired order if one secures an edition of the book with only one side of each leaf printed. The descriptions and keys are the work of three authors: the elepidote species have been worked out by H. T. Tagg of the Royal Botanic Garden, Edinburgh, the lepidote Rhododendrons by J. Hutchinson of the Royal Botanic Gardens, Kew, and the Azaleas and their allies by A. Rehder of the Arnold Arboretum. A considerable number of species are published here for the first time, most of them from

[1] The species of Rhododendron. Published by the Rhododendron Society. pp. 8 + 861. Ill. O. Edinburgh, 1930.—Price £1.10.



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GRAFT-BLIGHT OF LILAC

GRAFT-BLIGHT OF LILAC

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Graft-blight of Lilac

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Graft-blight of Lilac

Yunnan and some from Tibet, Burma or Assam; the names of the new species are the following: *Rhododendron Balfourianum* Forr. & Tagg, *R. glischroides* Forr. & Tagg, *R. hirtipes* Tagg, *R. rude* Forr. & Tagg, *R. vesiculiferum* Tagg, *R. chrysolepis* Hutch. & Ward, *R. deleiense* Hutch. & Ward, *R. mishmiense* Hutch. & Ward, *R. crebreflorum* Hutch. & Ward, *R. pruniflorum* Hutch. & Ward, *R. tsangpoense* Hutch. & Ward, *R. peregrinum* Tagg, *R. Hardingii* Forr., *R. paludosum* Hutch. & Ward, *R. imperator* Hutch. & Ward, *R. uniflorum* Hutch. & Ward, *R. ciliipes* Hutch., *R. notatum* Hutch., *R. scopulorum* Hutch., *R. taronense* Hutch., *R. Taggianum* Hutch., *R. dumicola* Tagg & Forr., *R. vellereum* Hutch., *R. eurysiphon* Tagg & Forr., *R. docimum* Balf. f., *R. vestitum* Tagg & Forr., *R. cerasinum* Tagg, *R. concinnoides* Hutch. & Ward, *R. bauhiniiflorum* Watt, *R. flavantherum* Hutch. & Ward, *R. pleistanthum* Balf. f., *R. asperulum* Hutch. & Ward, *R. insculptum* Hutch. & Ward and *R. exasperatum* Tagg. Besides these new species two new names are proposed: *Rhododendron Makinoi* Tagg for *R. stenophyllum* Makino, not Hook. f., and *R. hongkongense* Hutch. for *Azalea myrtifolia* Champ.

The chief value of the work lies in the fact that here for the first time the large number of Rhododendrons discovered and described chiefly from western China during the last 50 years have been brought together in one volume and made readily available for the botanist and for the lover of these highly ornamental plants. The fact that the descriptions are drawn up according to a uniform scheme makes comparisons of the descriptions of the different species easy and thus facilitates identification.—A. R.

Illustrations of Eucalyptus.—Under the title "An anthography of the Eucalyptus" Russell Grimwade[1] has published an attractive volume containing descriptions and monochrome plates of 103 species of Eucalyptus. The plates are reproductions of characteristic photographs of flowering and fruiting branches and the monochrome print brings out beautifully the color of the flowers which vary from white to yellow and pink or red. The text accompanying the plates contains notes on the discovery of the species, their distribution, economic importance and other points of interest and in the non-technical description the characters not apparent or clearly seen on the plate are emphasized. In an introductory chapter the history of the genus is dealt with and its distribution, botanical characters, vernacular names and economic properties. The work is primarily intended for the horticulturist, nature lover, forester and grower of Eucalyptus, but also the botanist will find

[1] GRIMWADE, RUSSELL. An anthography of the Eucalyptus [Ed. 2] 22 + 8, 103 pl. O. Angus & Robertson, Ltd., Sydney, 1930.—Price £2.2.

much of value and interest in the volume and particularly will he find the plates often helpful in the identification of species, though for detailed description and classification he will have to turn to J. H. Maiden's voluminous Critical revision of the genus Eucalyptus. The first edition of the Anthography appeared in 1920; it had only 80 plates and less full descriptions.—A. R.

Pandorea nervosa Van Steenis, n. sp.
A. Habit (½ nat. size). B. Cross section of the ovary (magnified).

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A PREVIOUSLY UNDESCRIBED PANDOREA FROM NORTHEAST QUEENSLAND, AUSTRALIA

C. G. G. VAN STEENIS

Plate 35

Pandorea nervosa Van Steenis, n. sp.

Pandoreae jasminoidi similis sed foliis utrinque reticulato-venosis, nervis venisque utrinque prominentibus, calyce in alabastro clauso deinde irregulariter in lobis rumpente, corolla infundibuliforme, albida, tubus intus secus basin pallide flavescente, lobis minoribus differt.

Vine with slender, ribbed, purple stems minutely puberulous towards the top. Leaves with 5 leaflets, those immediately below the thyrse reduced to 3 leaflets; petioles 1.5–3.5 cm. long, slightly sulcate towards the tip as the rhachis, the bases of each pair connected with a prominent rim; rhachis ca. 2 cm. long; petioles of the lateral leaflets sulcate and winged by the decurrent margin of the blade, 2–5 mm. long, articulated at the insertion, those of the terminal leaflet (in the 2-jugate leaves) 1–1.5 cm. long, those in the 1-jugate leaves nearly sessile on and articulated with a stalk (rhachis) 1 cm. long. Leaflets dark green, ovate to ovate-oblong, the base rounded or rather cuneate, decurrent along the petiole, the tip rather abruptly acutely acuminate or even shortly caudate (acumen up to 1 cm. long), blade mostly oblique, 2.5–6 cm. long and 1.5–4 cm. broad; margin entire or with 1–2 crenate teeth on each side below the acumen; midrib sulcate above, rather strongly prominent below; primary nerves 5–7 pairs and a few smaller ones in the acumen, curved upwards towards and along the margin and united in a looped line, when dry prominent on both sides as are the numerous reticulations; glands impressed on the upper surface, dark-colored and not immersed below. Peduncle terminal, protruding ca. 2 cm. above the reduced upper leaves, as long as the rhachis. Thyrse minutely puberulous throughout, dense-flowered; lateral stalks opposite, the lower ones ca. 5 mm. long, 3-flowered, the upper ones (sometimes all in the poorer specimens) 1-flowered. Bracts acute-triangular, 1–1.5 mm. long, the bracteoles smaller.

Pedicels 3–6 mm. long, articulated below the thickened obconical hypanthium supporting the calyx. Flowers odorless, showy. Calyx glabrous, closed in bud with indistinctly indicated lobes, later on irregularly split into lobes up to 2.5 mm. high, campanulate, 6–7.5 mm. high (measured from the articulation). Corolla white, the tube with yellow inside near the base, infundibuliform, slightly curved, ca. 3.5 cm. long (excluding the lobes), puberulous-papillose outside, the slightly inflated broad base glabrous, the lower half of the tube inside long-pubescent at the side of the fertile stamens, glabrous at the opposite side near the staminodium; lobes 5, slightly unequal, broadly rounded, suborbicular, 7–9 mm. high, 7–11 mm. diameter, papillose-puberulous on both surfaces. Stamens 4, the smaller ones on filaments about 7 mm. long, inserted about 6 mm. above the base of the tube, the filaments of the longer ones 12–13 mm. long, inserted at about 9–10 mm. height, all glabrous except at their glandular-hairy insertion. Anthers divergent, linear-oblong, rather blunt, 3.5 mm. long, the connective indistinctly protruding above the cells. Staminodium small, curved, linear. Disk entire, annular-cupular, surrounding the base of the ovary. Ovary oblong, 6 mm. high, more or less terete, 2-celled, each cell with several rows of ovules, each row with 10–15 ovules; style linear, ± 1.5 cm. long, stigma with 2 blunt spathulate lobes. Dissepiment bearing 2 prominent placentas in each cell. Fruit unknown.

NORTH QUEENSLAND: Ghurka Pocket, Boonjie, Atherton Tableland; common in rain-forest, 700 m. alt., *S. F. Kajewski*, no. 1227 (Arnold Arb. Exped.), Sept. 24, 1929 (vine growing over small trees, leaves dark green, stems purple, flower white with light yellow inside near the base, very showy but no perfume).

This is the fourth Australian species of *Pandorea*. It is allied to *P. jasminoides* K. Schum. and can be inserted into the key given in my monograph of the Australian Bignoniaceae (Proc. Roy. Soc. Queensland, XLI. 39–58. 1928) as follows:

1a. Corolla large, 4–5 cm. long, outside papillose-puberulous. . . . . .1b.
Corolla 1–1.5 cm. long, glabrous outside. . . . . .2.

1b. Corolla white with light yellow inside near the base of the infundibuliformous tube, the lobes suborbicular, ca. 1 cm. in diameter. Calyx 6–7.5 mm. long, closed in bud, later on split irregularly into lobes up to 2.5 mm. long. Leaflets ovate to ovate-oblong, distinctly and mostly abruptly acute-acuminate, the nerves and reticulations distinctly prominent. . . . .*P. nervosa.*
Corolla creamy or pale rose, streaked with carmine in the throat, the tube hypocraterimorphous, the lobes suborbicular, ± 2 cm. in diameter. Calyx 5–6 mm. high, open in bud, remaining truncate. Leaflets oblong to lanceolate, rarely some ovate, with a blunt, gradually tapering tip, the nerves and reticulations not or slightly visible.
P. jasminoides.

A prominent nervature is known in *Pandorea* only in the entirely different *P. stenantha* Diels from New Guinea and *P. Baileyana* Van Steenis from New South Wales. The form of the corolla is the same as in *Tecomanthe* and the lobed, large calyx is aberrant in *Pandorea;* the corolla-tube, however, being long-pubescent on the anterior side and the inflorescence being a thyrse (not a raceme as in *Tecomanthe*) I found it advisable to refer it to *Pandorea*. For the rest I have already pointed out elsewhere (Bull. Jard. Bot. Buitenzorg, sér. 3, x. 202. 1928) that there seems to be no important difference between *Pandorea*, *Tecomanthe* and *Campsis* but I feel not competent to unite these genera as I had no opportunity to make a closer study of *Campsis*, this being the oldest genus described.

As appears from the key *P. nervosa* is related to *P. jasminoides* K. Schum., the latter species having no large range of variability as contrasted with *P. pandorana* Van Steenis which is exceedingly variable.

I do not know the description of *Tecoma doratoxylon* J. M. Black (Transact. & Proc. Roy. Soc. S. Austral. LI. 383. 1927) because this periodical is not accessible to me but I suspect that it will be another species of *Pandorea* or *Tecomanthe*.

HERBARIUM, BUITENZORG
JAVA

NOTULAE SYSTEMATICAE AD FLORAM SINENSEM, III

H. H. HU

Fagus lucida Rehder & Wilson in Sargent, Pl. Wilson. III. 191 (1916).

Descriptioni adde: Involucrum 6–9 mm. longum, fulvo-tomentulosum, extus squamis adpressis deltoideis brevissimis acutis munitum, nuculis exsertis fulvo-sericeo-pubescentibus 9 mm. longis, pedunculo gracili 1 cm. longo glabro suffultum.

Involucre 6–9 mm. long, tawny-brown-tomentulose, with very short appressed acute deltoid scales on the outside, nut exserted, tawny-sericeous-pubescent, 9 mm. long; stalk slender, 1 cm. long, glabrous.

KWANGSI: Dar Young Kiang, Luchen, border of Kweichow, 1300 m., *R. C. Ching*, Kwangsi Exped. Metrop. Mus. Nat. Hist. Acad. Sin. no. 6272, June 27, 1928.

The specimen collected in Kwangsi agrees exactly with the type from Hupeh in the leaves having sinuate margins with secondary veins projecting from the bases of the sinus forming triangular teeth, but differs in the midribs and secondary veins beneath being glabrous, while the midribs above are pilose.

It is very satisfactory to have been able to collect the fruits and to publish a supplementary description of this interesting species which Rehder & Wilson first published fourteen years ago based on sterile specimens. This species is striking also in the involucre being covered not with recurved prickles but with very short appressed deltoid scales, a character very rare in the genus *Fagus*, which easily differentiates this from all other eastern Asiatic species. It is very common in the woods on the top of Dar hills above Dar Young Kiang.

Hydrangea kwangsiensis, sp. nov.

Frutex 1 m. altus, ramulis gracilibus teretibus glabris. Folia membranacea, oblanceolata vel lanceolata, 7–10 cm. longa et 1.8–2.8 cm. lata, acuminata, basi cuneata et decurrentia, margine leviter revoluta et satis remote minuteque callosa-denticulata, glabra, supra laete viridia et costa leviter elevata, subtus pallide viridia, costa magis elevata et venis lateralibus curvatis vix distinctis; petioli 8–10 mm. longi, glabri. Cymae planae, satis multiflorae, ad 14 cm. longae et 8–9 cm. latae, longe pedunculatae pedunculo circiter 5 cm. longo gracili, radiis 3–5 oppositis, basi bracteis parvis foliaceis suffultis, axibus pedicellisque minute crispulo-villosis; pedicelli graciles, 1.5–2 mm. longi; flores steriles pauci, sepalis 4 albis rhombico-ovatis vel suborbicularibus 11 mm. longis latisque ad marginem crispatis; flores fertiles coerulescentes, tubo calycis turbinato minute hispidulo, dentibus triangularibus, petalis late ovatis apice rotundatis 2 mm. longis, staminibus 10 subaequalibus quam petala brevioribus; ovarium semi-superum; styli 3 recurvi. Fructus ignotus.

Shrub to 1 m. high; branchlets slender, terete, glabrous. Leaves membranaceous, oblanceolate to lanceolate, acuminate, cuneate and decurrent at base, slightly revolute and rather remotely and minutely callose-denticulate, glabrous, light green and with slightly elevated midrib above, pale green and with more prominently elevated midrib and very faint lateral arching veins beneath, 7–10 cm. long, 1.8–2.8 cm. broad; petiole glabrous, 8–10 mm. long. Cymes flat, many-flowered, to 14 cm. long, about 8–9 cm. broad, composed of 3–5 opposite radii with small leafy bracts at the base, long-peduncled with the peduncle about 5 cm. long, rachis of the cyme and pedicels minutely crisp-villose; pedicels slender, 1.5–2 mm. long; sterile flowers few, sepals 4, white, rhombic-ovate to suborbicular, crisp along the margins, 11 mm. long and broad; fertile flowers bluish; calyx turbinate, minutely hispidulous, teeth triangular; petals broadly ovate, rounded at apex, 2 mm. long; stamens 10, subequal, shorter than the petals; ovary half-superior, style 3, recurved. Capsule unknown.

KWANGSI: Chu-feng Shan, north of Luchen Hsien, on border of Kweichow, alt. 800 m., very common in woods or in open thickets, *R. C. Ching*, Kwangsi Exped. Metrop. Mus. of Nat. Hist. Acad. Sin. no. 5386 (type), June 8, 1928.

A species of the section Euhydrangea, allied to *H. yunnanensis*, Rehd. differing in the leaves being minutely callose-denticulate and with very faint lateral veins, in the long-peduncled cyme and in the smaller sterile flowers.

Citrus kwangsiensis, sp. nov.

Arbor ad 10 m. alta, trunco 25 cm. diam., cortice viridi-cinereo; ramuli longi, irregulariter angulati, striati, lenticellis sparsis ovalibus muniti, sparse pilosuli, virides; spinae validae, pungentes, 8–12 mm. longae. Folia coriacea, elliptico-oblonga, 9–15 cm. longa et 4–6.5 cm. lata, apice obtusiuscula, basi late cuneata vel rotundata, irregulariter dupliciter adpresseque crenulato-serrulata, glabra, supra intense viridia et venis non prominentibus, subtus pallide viridia, et venis elevatis reticulata; petioli articulati, anguste alati, 12–15 mm. longi, sparse pilosuli. Flores ignoti. Fructus immaturus ovoideus, leviter obtuse apiculatus, 3–5 cm. diam., 13-locularis, cortice 11 mm. crasso glabro, pulpa exigua 1.5 cm. diam.; fructus maturus 7 cm. diam., luteus (fide collectoris).

Tree to 10 m. high, 25 cm. in diam.; bark greenish-grey; branches long, irregularly angular, striate, with scattered oval lenticels, sparsely pilosulous, green; spines stout, sharp, 8–12 mm. long. Leaves coriaceous, elliptic-oblong, obtusish at apex, broadly cuneate to rounded at base, irregularly doubly and appressed-crenulate-serrulate along the margins, glabrous, intensely green and with non-prominent veins above, paler green and with elevated and reticulate veins beneath, 9–15 cm. long, 4–6.5 cm. broad; petiole articulate to the blade and the twig, narrowly winged, 12–15 mm. long, sparsely pilosulous at base. Flowers unknown. Young fruit ovoid, slightly obtusely apiculate at apex, 3.5 cm. in diam., rind 11 mm. thick, glabrous, pulp scanty, 1.5 cm. in diam., 13-segmented; mature fruit 7 cm. in diam., yellow (fide collector).

NORTH KWANGSI: Hoo-chi, alt. 900 m., cultivated in garden, *R. C. Ching*, Kwangsi Exped. Metrop. Mus. Nat. Hist. Acad. Sin. no. 6456 (type), June 14, 1928.

A very distinct species apparently related to *C. medica* L. and *C. maxima* Merr. by its fruits having very thick rind, but differing from the former in the articulated and narrowly winged petioles and from the latter in narrowly winged petioles and much smaller fruits.

Acer angustilobum, sp. nov.

Arbor ad 14 m. alta, trunco 30 cm. diam., cortice cretaceo-albo; ramuli graciles, glabri. Folia chartacea, 3–5-lobata, ad 15 cm. longa et 13 cm. lata, basi cuneata vel subrotundata, lobis lanceolatis longe caudatis apicem versus remote serrulatis, lobo medio ad 6.5 cm. longo et 2.2 cm. lato, lateralibus paullo brevioribus et angustioribus, basalibus parvis ad 1.5 cm. longis, sinubus acutis, lamina utrinque clare et lucide viridi, axillis subtus albido-barbatis exceptis glabra, utrinque reticulato-venulosa; petioli graciles, ad 4 cm. longi, glabri. Inflorescentia paniculata, ad 11 cm. longa; samarae virescentes, alis horizontaliter patentibus, nuculis inclusis 3 cm. longae et 1 cm. latae, basi distincte angustatae, dorso curvatae, nuculis ellipsoideis leviter compressis sublaevibus leviter tantum venulosis, 6 mm. longis et 3.5 mm. latis.

Tree to 14 m. high, 30 cm. in diam.; bark chalky white; branchlets slender, glabrous. Leaves chartaceous, 3–5-lobed, cuneate or subrounded at base, to 15 cm. long, 13 cm. broad, lobes lanceolate, long-caudate at apex, with acute sinuses, remotely serrulate toward the apex, midlobe to 6.5 cm. long, 2.2 cm. broad, lateral lobes slightly shorter and narrower, basal lobes small, to 1.5 cm. long, 7 mm. broad; pale shining green on both surfaces, glabrous except with axillary tufts of whitish hairs beneath, reticulate-venulose on both surfaces; petiole slender, to 4 cm. long, glabrous. Panicles elongated, to 11 cm. long; samaras greenish, with wings horizontally spreading, including the nutlets about 3 cm. long, 1 cm. broad, distinctly narrowed at base and arching at back, nutlets ellipsoid, slightly compressed, rather smooth, only slightly venulose, 6 mm. long, 3.5 mm. broad.

Kwangsi: Chu-feng Shan, north of Luchen Hsien, alt. 630 m., common in woods, *R. C. Ching*, Kwangsi Exped. Metrop. Mus. Nat. Hist. Acad. Sin. no. 5802 (type), June 8, 1928.

A species of the section Spicata, allied to *A. sinense* Pax and *A. Wilsonii* Rehd., differing from the former in the 3–5 narrow ascending lobes remotely serrulate toward the apex and in the blade being narrowed toward the rounded base and from the latter in the leaves often 5-lobed with two small basal lobes.

Acer oblongum Wall. var. **macrocarpum,** var. nov.

A typo recedit folius subtus minute tomentulosis, corymbo fructibus 4–5, pedunculo permanenter floccoso, samarae ad 4 cm. longae, alis semiorbicularibus 3.2 cm. longis et 1.4 cm. latis, basi abrupte contractis ad marginem irregulariter erosis, nuculis ad 7 mm. longis.

Differing from the type in leaves being minutely tomentulose beneath, cymes with 4–5 fruits, peduncle persistently flocoose, samara to 4 cm. long with semi-orbicular wings 3.2 cm. long, 1.4 cm. broad, irregularly erose along the margins and abruptly contracted on the lower part, and nutlets to 7 mm. long.

KWANGSI: Tang-Chia-Fu, east of Luchen Hsien, alt. 300 m., rare in woods, *R. C. Ching*, Kwangsi Exped. Metrop. Mus. Nat. Hist. Acad. Sin. no. 5220 (type), May 23, 1928.

Rhododendron minutiflorum, sp. nov. (§ Tsutsuti)

Frutex erectus ad 2.25 m. altus, ramosissimus; ramuli verticillati, ascendentes, tenues tortuosi, vestigiis fuscis setarum scabridi, juniores strigoso-setosi setis applanatis rubro-fuscis appressis. Folia persistentia, 4 vel 5 in apice ramulorum congesta, crasse chartacea, late obovata vel oblonga, 7–11 mm. longa et 4.5–5.5 cm. lata, basi cuneata, apice breviter acuminate, margine revoluta et minute crenulata, supra obscure viridia et strigoso-setosa, subtus pallide viridia et glabra costa margineque strigoso-setosis exceptis; petiolo strigoso-setosi; ad 2 mm. longi. Flores simul cum foliis novellis, in umbellis terminalibus 3-floris; bracteae minutae, triangulares, acutae; pedicelli strigoso-setosi, ad 2 mm. longi; calyx dense pilis strigosis obtectus et ciliatus, lobis subrotundatis circa 1 mm. longis et 1.5 mm. latis; corolla 7 mm. diam., rotato-infundibuliformis, tubo extus pilis rubescentibus pilosulo intus glabro 2.5 mm. longo, lobis patentibus tubum subaequantibus ovato-oblongis breviter acuminatis 3 mm. longis basi 2.5 mm. latis utrinque glabris non maculatis; stamina 5, subaequalia, exserta, filamentis circa 7 mm. longis triente superiore excepto minute puberulis, antheris oblongis 1 mm. longis; ovarium dense setosum, 2.5 mm. longum; stylus declinatus, 8 mm. longus, rubido-pubescens, stigmate capitato. Capsula ignota.

Erect shrub to 2.25 m. high; branchlets dense, verticillate, slender, tortuous and arching, scabrid with blackened remains of old appressed bristly hairs, young growth strigose-setose with reddish-brown flattened bristly hairs. Leaves persistent, those of this year's growth 4 or 5 crowded at the apex of the branchlets just above those of last year, thickly chartaceous, broadly obovate to oblong, cuneate at base, shortly acuminate at apex, revolute and minutely crenulate and the margins, dark green above and strigose-setose above, paler green and glabrous except densely strigose-setose along the midrib and the margins beneath, 7–11 mm. long, 4.5–5.5 mm. broad; petiole strigose-setose, to 2 mm. long. Flowers appearing with the leaves, in terminal 3-flowered umbels; bracts minute, triangular, acute; pedicels strigose-setose, 3–4 mm. long; calyx completely covered by and fimbriate along the margins with dense bristly hairs, lobes distinct, roundish, rounded at apex, about 1 mm. long and 1.5 mm. broad; corolla 7 mm. in diameter, rotate-funnel-shaped, tube pilosulous with reddish hairs outside, glabrous inside, 2.5 mm. long, lobes spreading, about as long as the tube, ovate-oblong, shortly acuminate, 3 mm. long, 2.5 mm. broad at base, glabrous on both surfaces, not spotted; stamens 5, subequal, exserted, about 7 mm. long, minutely puberulous on the lower ⅔ of their whole length; anthers oblong, 1 mm. long; ovary completely concealed by dense bristly hairs, 2.5 mm. long; style declinate, pubescent with reddish hairs, 8 mm. long; stigma capitate. Capsule unknown.

This is a very distinct species of the section Tsutsutsi; in its flowers it resembles *R. Seniavinii* Maxim., except that they are much smaller, but the leaves are very different and by their size recall those of *R. serpyllifolium* A. Gray which, however, has entirely different flowers.

KWANGSI: Chu-feng shan, north of Huchen hsien, alt. 1120 m., *R. C. Ching*, Kwangsi Exp. Metrop. Mus. Nat. Hist. Acad. Sin. no. 5860 (type). June 9, 1928.

Porana sinensis Hemsley in Jour. Linn. Soc. XXVI. 167 (1890).
Vatica cordata Hu in Jour. Arnold Arb. XI. 225 (1930).

In describing this species I had overlooked that the genus *Porana* has a fruit very similar to that of the section Synaptea of the genus *Vatica*. The presence of only fruiting specimen caused this error.

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AMORPHA BRACHYCARPA E. J. Palmer, sp. nov.
Photograph of the type specimen